The ecology and breeding behaviours of urban Sparrowhawks *(Accipiter nisus)* in Edinburgh, Scotland

by

Michael J. McGrady

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ABSTRACT

Edinburgh has 20-35 breeding pairs of Sparrowhawks. Their ecology is similar to those living in rural areas (See: Newton 1986). House Sparrows were the most important Sparrowhawk prey: 27% of prey items, and 22% of biomass. Sparrowhawks fed on whatever prey, within a certain size range, was available. The mean nearest-neighbour distance was 1.3 ±0.08 km. There was no indication that the composition of the population differed from that found in the rural areas. Adult female survival was 53%, yearling survival 41%. Pollutants were not particularly high. The average residency for a breeding female Sparrowhawk was 1.4 yrs, and 1.5 yrs for the male. 54% of all trapped females were new recruits to the breeding population.

Range sizes varied with season, age and sex of individuals. The mean range size for breeding, adult males was about 400 ha. Range size could be affected by roosting behaviour. Some breeders roosted up to 2 km away from their nesting place. Range size of yearlings was directly related to the number of roost sites used, which increased as egg-date approached. This was interpreted as prospecting for openings in the breeding population.

51 potential nesting places were identified, 39 were occupied in the 4 years. Some nesting places were preferred. On average, 24 nests produced eggs/yr, 3.94 eggs/nest were laid, 2.47 chicks hatched/nest, and 2.3 fledged/nest. Wet, cold weather in spring and summer decreased production. Production was affected by the turnover of breeding females. Other causes of variation, including human disturbance, could not be proven.

The breeding behaviours of Sparrowhawks were observed and interpreted in terms of the possible reproductive strategies of the individuals. Breeding male and female Sparrowhawks spent more time at the nesting place as egg-date approached, and more time together in the morning and late afternoon. Mate guarding could not be proven. Displays increased as egg-date approached, and were more common in the morning. Courtship feeding increased as egg-date approached. Food presentations by the male were mostly made in the morning. Copulations showed similar seasonal and diurnal variation to the other behaviours. Copulation rates were high (150-250/clutch). There was no concrete evidence that the male was buying copulations

with food presentations. All behavioural rates were affected by breeding birds roosting at the nesting place together later in the season.

13% of all copulations were extra-pair, and occurred when an intruding female (which was paired with another male) solicited a territory holding male. Sperm storage tubules were identified in the reproductive tract of female Sparrowhawks. Chicks were produced which were not the offspring of the male with which the female was 'paired'.

--- To the memory of Charles W. McGrady Jr.

ACKNOWLEDGEMENTS

Particular thanks goes to Iain Taylor and Ian Newton who suffered (seemingly unflinchingly) through all my trials from the beginning to the end. If it were not for them, I could not have completed this work. I'd like to thank George Carse. What else can I say? He's one of a kind! To Graeme Anderson and Derek Triplett, whose tree-climbing abilities had to be seen to be believed, I shall never climb a tree again without thinking of them. Thanks go to the people of the University of Edinburgh, and the then Department of Forestry and Natural Resources for all their support. Also, Roy Carter whose enthusiasm for the intracacies of Sparrowhawk DNA amazes me. The Institute of Terrestrial Ecology provided me with the results of pesticide analyses of both Sparrowhawk corpses, and eggs. Ian Wyllie provided more than useful comments on drafts of this thesis, for which I am grateful. I am grateful to the American Friends of Edinburgh University for their financial assistance. Of course, this study could not have been done without the goodwill of the people of Edinburgh, particularly those who put up with me climbing into their gardens, and up their trees. I am very grateful for the support of my family. Their far-away support was vital. Finally, and equally importantly, I am grateful to the friends I'll always have, particularly, Neil, Stuart, Clare, Morag, Lindsey, Elaine, Justin, Yvonne, and Martina. Unfortunately, space limits the number of people I can thank here. The help and humour of all those people, given freely, allowed me to get not only the most out of the study, but the most out of life in Britain.

I learned today that my ornithology had done no service. That birds I heard, which fortunately did not come within the scope of my science, sung as freshly as if it had been the first morning of creation, and had for background to their song an untrodden wilderness, stretching through many a Carolina and Mexico of the soul.

- Henry David Thoreau

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CHAPTER 1

Study Area, General Methods and Terminology

Introduction

This thesis investigates the general ecology of a population of Eurasian Sparrowhawks (*Falconiformes Accipiter nisus*) that has recently colonized the city of Edinburgh, Scotland. It also looks at the behaviours associated with breeding in this small predator. The movement of the Sparrowhawk into urban areas is only a recent development, and it is probably only now that the conditions are favourable (expanding population and diminishing numbers of stereotypic rural habitats) for this colonization.

The Sparrowhawk is one of the best known of all the raptors. Besides being widely studied in different areas for short periods of time, the Sparrowhawk has also been the subject of long-term investigations. Recently, Newton (1986) collected the information from these studies (both long and short) into one volume. This volume, which includes data from his own, long-term study of Sparrowhawks in southern Scotland, describes the ecology, and natural history of the Sparrowhawk in detail. It is the basis for this study, with which it is compared and contrasted.

Although detailed by Newton (1986), it might be helpful to give some general characteristics of Sparrowhawks (See also: Owen 1916-1937; Cramp *et al.* 1980). The Sparrowhawk is the smallest of the Palearctic accipiters. Adult males and females are distinct both in plumage and in size, but in both sexes these characteristics are somewhat variable. The adult male is grey to blue-grey in colour dorsally and barred fine orange to orange-brown on a white to cream chest. The amount of orange-brown on the chest is variable. The adult female is more brown dorsally, and the ventral barring is usually thicker and browner. Like many other birds of prey, the Sparrowhawk displays reversed sexual size dimorphism. Indeed, they are the most size dimorphic of

all raptors for which measurements have been taken. In the late spring, when the female is at her heaviest, she may weigh more than twice as much as her mate (Plate 1.5).

Yearlings and adults are seperable by plumage but not by size. Yearlings (of both sexes) resemble females in colouration. Yearling and adult females are only sometimes distinguishaabel in the field. In the hand, the plumage of the juveniles is browner dorsally, and the dark body abd flight feathers or the juvenile are tipped rust. The chest and belly of the juveniles display brown heart or tear shaped markings. Juvenile wings are marginally longer and less rounded than those of the adults (Cramp and Simmons 1980)

The Sparrowhawks range includes virtually all of the Palearctic as well as the northern parts of the African continent. The Sparrowhawk is migratory in the northern part of its range. It is not in Britain. In Britain, its closest relative is the larger Goshawk (*A. gentilis*), and within the western Palearctic its range overlaps the ranges of two other accipiters, the Levant Sparrowhawk (*A. brevipes*) and the Shikra (*A. badius*).

Sparrowhawks are birds of the woodland and woodland edge. They are particularly adapted for life here, where they nest and catch the avian prey which makes up over 99% of their diet. Even within the city where they may hunt in more open areas, trees are still required for nesting. They will prey upon birds ranging in size from about 5 g (e.g. Goldcrest *Regulus regulus*) to over 400+ (e.g Wood Pigeon *Columba palumbus*) (Newton 1986).

The fortunes of the Sparrowhawk population within Britain have been mixed. Throughout the early part of the century they were persecuted quite heavily by gamekeepers, a persecution which ceased temporarily during the Second World War. Indeed, early notes on the species were sometimes coincidental with game keeping activities. (See: Owen 1916-1937). After the war, persecution resumed, and the advent of certain pesticides was linked to reduced production in the Sparrowhawk (and other species), so that throughout most of the 1960's the population was in serious decline. Since the banning of some of these harmful pesticides in Britain, the population of the Sparrowhawk has been on the increase.

Today, the Sparrowhawk is a widely distributed, common raptor in Britain (probably second only to the Kestrel (*Falco tinnunculus*) in numbers) (Newton 1986). The

recovery from the pesticide years has been so complete that Sparrowhawks have started to colonize areas where they were not found before the introduction of pesticides such as some of the cities in Britain and other parts of Europe. Edinburgh, Dundee, Birmingham, Glasgow, and Bristol all contain a population of breeding Sparrowhawks. On the continent, Prague, Cologne, and Warsaw also have urban populations of Sparrowhawks. Other cities probably have nesting populations, although their nesting densities must vary with the amount of suitable nesting places.

Initially, the focus of this study was the general ecology of the Sparrowhawk within the city environment. As the study progressed, it was noted that many of the habits of the urban population were similar to those studied in the rural areas (See: Newton 1986). Food habits were similar (Chapter 2) as were many of the details of their breeding biology (Chapter 5). These similarities argued that the urban population was not significantly different from the extensively studied rural populations.

However, unlike rural populations, which were difficult to observe both because of their forest habitat and secretive nature, the city Sparrowhawks were,to some extent, habituated to the presence of humans, and could be approached much more closely. This 'tameness' in conjunction with the fact that most nesting habitat available to the Sparrowhawks within the city was small and often not very densely forested (Plate 1.4), allowed behaviours at the nest to be observed at a number of sites without disturbing the breeders (Chapter 6). So, while data was collected on the city Sparrowhawks which could be compared to similar data on those in rural areas, new information on the behaviours of paired and unpaired Sparrowhawks during the pre-laying phase of the breeding season could also be gathered and examined.

The Study Area.

The study area was the urban area of Edinburgh bounded on the north by the Firth of Forth, the city bypass road to the west and south, and the town of Musselburgh to the east, an area of 265 km^2.

Edinburgh is located on the eastern coast of Britain at 55^o 57' latitude 3^o 13' longitude. The city has a population of some 440,000, and is the capital of Scotland. The main industries are business, tourism and government.

The study area is comprised of 11.6% woodland, and 17.5% grassland (See Plate 1.2). The rest of the area was occupied by buildings, roads, water, and open ground that was not covered in vegetation.

Woodland within the city was variable, both in species composition, shape, and size. Some trees were planted for primarily ornamental reasons. In some gardens, such as the Royal Botanic Gardens, exotic trees and shrubs were much more common than the species normally found in the countryside surrounding the city. Indeed, some of the species of plants on some of the territories do not grow naturally in the normal Palearctic range of the Sparrowhawk.

The shape of the areas covered by woodland also varied. In some cases, large numbers of trees were used to line roadways. These may have been useful to Sparrowhawks as corridors for hunting and commuting behaviours, but were of less use as suitable nesting areas.Still, these woodlands and gardens provided a suitable environment for year-round Sparrowhawk survival, and normal successful reproduction.

General Methods

Terminology

In most cases, terms used within this thesis are defined in the appropriate sections; many are as in Newton (1986). Clarification is given here of terms which are sometimes confused, and terms which describe the results of this particular study.

Nesting place is the immediate area around the nest which is usually vigorously defended by both breeders to the exclusion of other Sparrowhawks. In practical terms, no area except maybe the nest itself is totally exclusive. **'Nest'** and **'nest site'** are synonyms.

Potential nesting place is where an old nests or other evidence indicates that Sparrowhawks have used an area for nesting in the past.

Actual nesting place is where the presence of (at least) a nest structure indicates that Sparrowhawks attempted to nest in a given year.

The **pair** refers to the male and female which occupy a nesting place. **Non-pair** individuals could either occupy other nesting places or be non-breeders. Non-pair individuals seen at a nesting place were **intruders**.

During the spring-time, behavioural interactions between members of the pair resident at the nesting place where observations were being made were termed as **'within pair'** behaviours. Those interactions between at least on member of the resident pair and a non-pair individual are **'extra-pair'** interactions.

Plate 1.1 A satellite photograph of Edinburgh, the study area. Taken in 1979 from a distance of approximately 900 km. Landmarks: A= Arther's Seat; C= Corstorphine Hill; F= Firth of Forth.

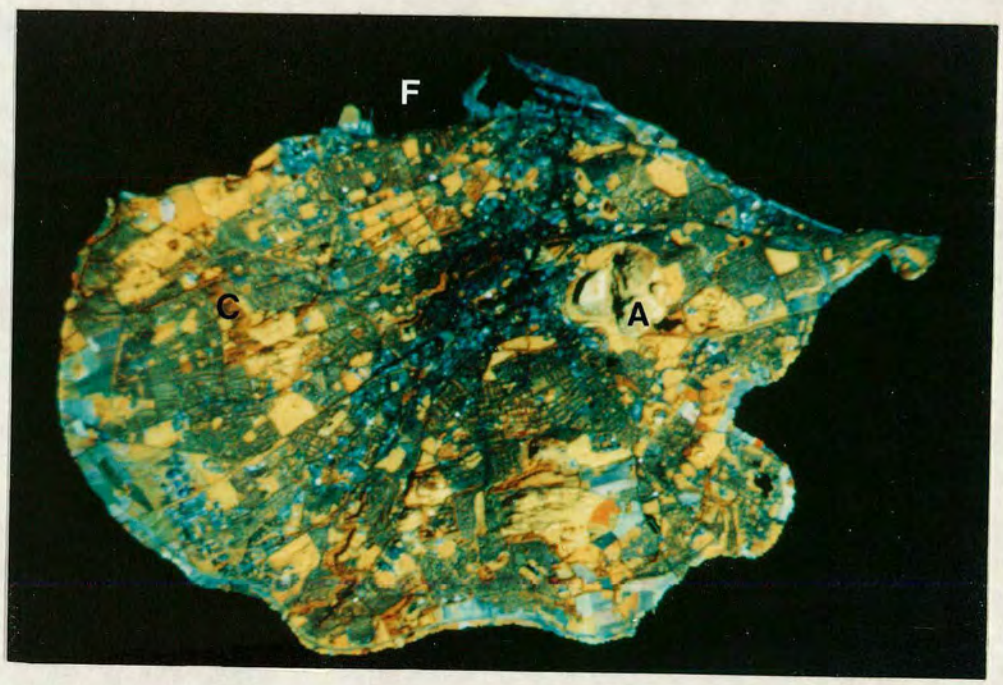
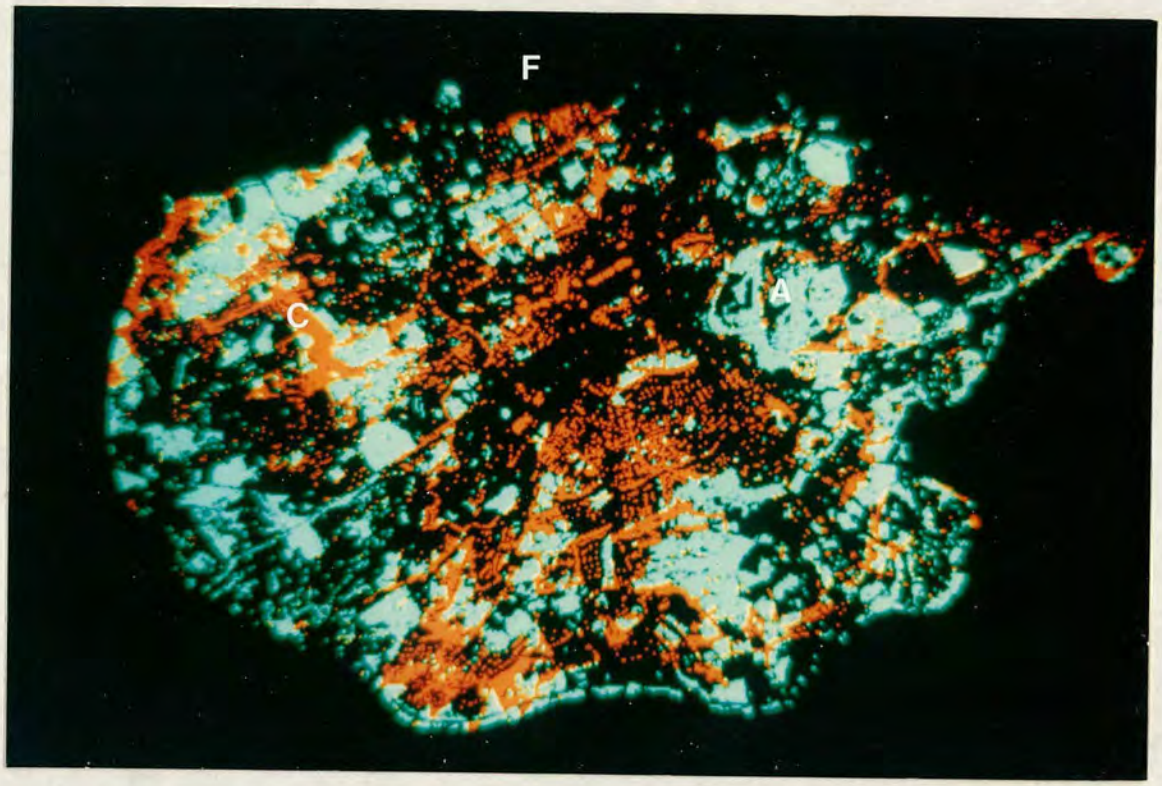


Plate 1.2 Satellite photograph of Edinburgh showing the wooded areas (red), and the areas of open ground and grassland (blue). Taken in 1979 from a distance of approximately 900 km. Landmarks: A= Arther's Seat; C= Corstorphine Hill; F= Firth of Forth.



For convenience, **breeders** were birds that bred within the study area, in a particular year, **Non-breeders** were those that did not breed in that year. It is probably the case that some Sparrowhawks moved out of the city and bred (or did not breed) there. Probably some 'non-breeders became 'breeders' after the study period. In one case a bird was classified as a breeder in two successive years, being a non-breeder in the interim.

Range was the area occupied by an individual or pair (Campbell and Lack 1985).

Territory will be used in its broadest sense being 'a defended area' (Campbell and Lack 1985). In the spring, for breeders, this is centred around the nest itself. this term is less applicable in the winter because defense is less obvious then. In that season the use of 'range' is more appropriate.

Roost, and **night-time roost** are used synonymously, and are places, usually in evergreen trees, where Sparrowhawks rested between dusk and dawn. **Day-time**

roosts were places where Sparrowhawks loafed during daylight hours. Principal roost was that place where a Sparrowhawk spent the largest proportion of its nights. **Secondary roosts** were those sites where a bird was known to have spent the night away from the principal site.

Reproductive strategy is the set of behaviours used by the Sparrowhawks to ensure their genes are passed on. The strategy is two-tiered, the reproductive strategy of the pair, and that of the individual. The two tiers are to a large extent defined and constrained by one another. To a certain extent the two tiers are defined by one another, So, because the ability of the individual to succeed is dependent on the pair's success, behaviours which maximize the chance of an individual's success are sometimes compromised by behaviours which promote the success of the pair. The most obvious behavioural compromise effects the male's ability to guard against cuckoldry; for although he must provide food for the female in the weeks prior to egg-laying, in doing so he leaves the nesting place and his mate un guarded against intruders.

Intruders were individuals Sparrowhawks which entered a territory which was not their own. In the spring, intruders could be either breeding at other nesting places or be non-breeders.

Floaters were those individuals which either did not attempt to breed or which failed early in the breeding attempt, and did not re-nest. Floaters were possible replacements for individuals lost to the breeding population.

Turnover was the change of resident breeder at a particular nesting place from one year to the next. Turnover could occur when a resident breeder died, and was replaced, when a residential breeder moved to another nesting place and bred, or when a resident breeder left a nesting place, was replaced, but did non breed.

Recruitment was when new individuals entered the breeding population, and was a component of turnover

Sparrowhawks can be divided in the field into two age classes, first year birds, and those that are more than one year old. These classes are distinguishable by plumage in the field for both sexes. In this thesis I use the term 'yearling', and 'adult'. **Yearling** was a bird which is in first-year plumage. Yearlings were able to breed, and some did so in

Edinburgh. **Adults** were birds more than one year old. These birds are generally in full adult plumage, although second year individuals retain a few yearling feathers. A two year old bird is only distinguishable from a >2-year old in the hand (See: Cramp and Simmons 1980; Newton 1986; and Section 1.1).

Males and females were always distinguishable in the hand, and in most cases when seen in the wild. The female Sparrowhawk is sometimes twice as heavy as the male. Adult males and adult females also differ in plumage (Plate 1.5). Yearlings of the two sexes were difficult to distinguish by plumage alone (See: Cramp and Simmons 1980; Newton 1986)

Locating Sparrowhawk territories

Within Edinburgh, a few Sparrowhawk nesting sites were known to local raptor enthusiasts (G. Carse pers. comm.), but because Sparrowhawks require trees in which to nest, some potential sites were identified using an ordinary tourist map of the city. City woodlands were searched for signs of attempted Sparrowhawk nesting (methods in Newton 1986), past or present, in all years. Throughout the study almost all woodland was searched. Some small stands of trees in backyard gardens were not searched, but many of these were never occupied by Sparrowhawks. Searching was carried out initially in the early breeding season, February and early March, but areas where no early indications of a breeding attempt were found were searched in April, May, and June as well. Searches were conducted in all years.

Given the persistent nature of Sparrowhawk nests, it was often possible to identify sites quite early in the year by their presence from previous years. As the breeding season approached though, sites could be identified by a concentration of the plucked feathers of the small birds upon which the Sparrowhawks preyed, and the stereotypic, white droppings of the Sparrowhawks themselves. Characteristically built new nests and/or the presence of a pair of Sparrowhawks in the late spring were indicative as well. After leaf-fall (November-December) places where nesting attempts were suspected, but could not be confirmed, were searched again (Plates 1.3 and 1.4).

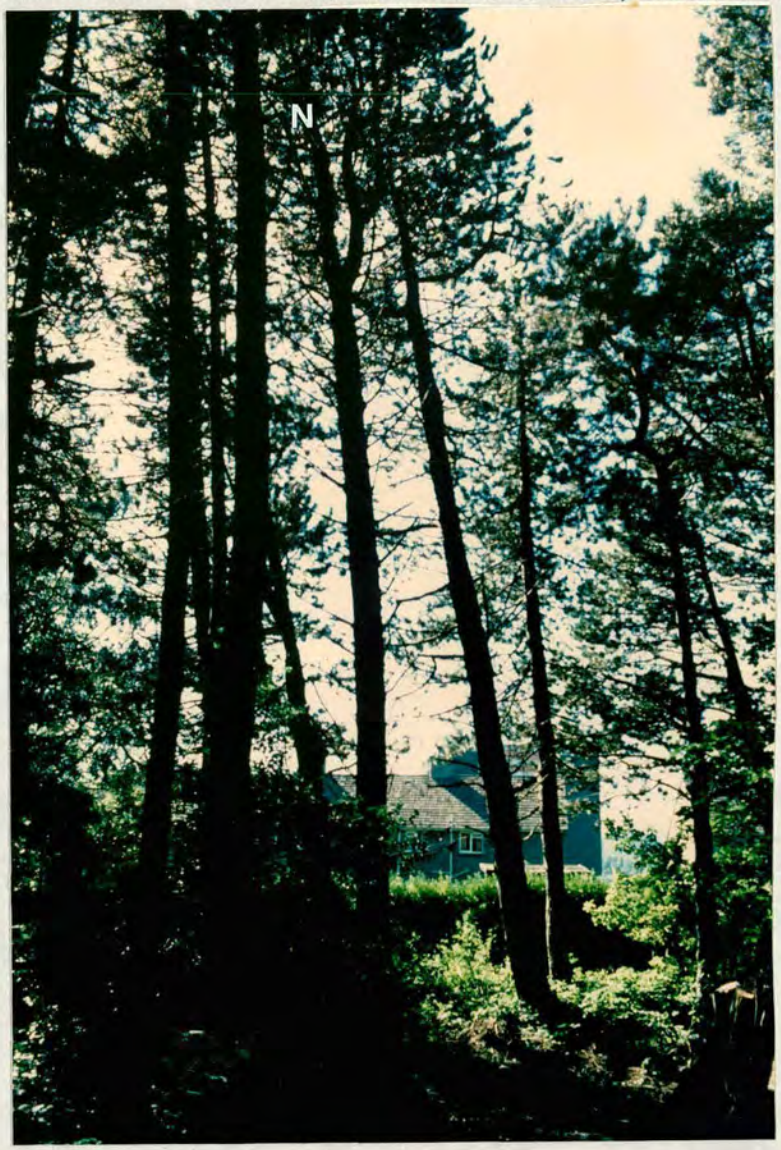
Plate 1.3 Sparrowhawk nest in a Lodgepole Pine *(Pinus contorta)* in a garden. N=Nest. In this nest, eggs yeilded 3 fledglings. This nesting place was occupied in all years of the study. "P"'s indicate trees used in other years.

Once the nest was located, the production of eggs, chicks, and fledglings was monitored by direct observation. This generally entailed climbing the nest tree three or four times a season. Unhatched eggs were collected for pesticide analysis.

Trapping methods

Once the sites were identified, an effort was made to trap the free-flying birds for individual marking, measurement and the sampling of blood for DNA finger printing analysis. See Chapters 5 and 6.

Plate 1.4 Sparrowhawk nest located in stand of Scot's Pine *(Pinus sylvestris)* planted as a wind-break. N=Nest. Three chicks hatched in this nest, none survived to fledging.



Trapping and marking methods, although fairly standard and similar to those of Newton (1986), were varied. Throughout the year (though primarily in the spring) free-flying Sparrowhawks were caught using a falling-lid trap, modified from a design by Kenward *et al.* (1983). During the breeding season, females were trapped at the nest. The nest tree was climbed while the female was incubating. The eggs were replaced with false eggs made from Plaster of Paris and painted as imitations. A noose carpet (See: Bloom 1987) was placed over the dummy eggs. When the female returned to incubate the clutch, she became ensnared in the nooses. Climbing the tree again, she and the trap

were retrieved, and the real eggs replaced in the nest. No adverse effects due to trapping were noticed. Often a trapped bird was back on the nest within 5 minutes of release.

An attempt was made to catch defensive Sparrowhawks at the nest using mist nets and *dho gaza* nets, stuffed owls and Sparrowhawks and taped calls (Clark 1981; Hammerstrom 1963), but with no success.

Processing trapped birds

The age and sex of trapped birds was determined, and they were individually marked. If they had been previously marked, the details of the tag were noted, and the identity of the individuals was determined subsequently.

Marking was achieved in several different ways, and any one bird might be marked in up to four different ways. All birds were fitted with British Trust for Ornithology rings made available under Permit. Further all non-nestlings had a unique number stamped on their flight feathers so their identity could be confirmed from moulted feathers. Numbers were stamped on using an ordinary changeable date stamp and permanent India ink. A subset of the birds were marked further using colour patagial markers (Village 1990) and leg streamers. Birds captured around a cluster of sites in the city centre in the early spring were colour marked to make it possible to recognize individuals for behavioural studies later on. There was no evidence of negative effects of marking birds (Chapter 6). Also in the spring, some birds were fitted with small radio transmitters (Chapter 4). Finally, the birds were weighed, a wing chord (flattened) measurement was made, a sample of blood was taken from the brachial vein, and released.

Collections of the moulted feathers of breeders were made so that if trapping failed, feathers of the breeders could be compared to the feathers moulted in previous years. The individual colour characteristics of the feathers allowed them to be used to identify individual birds without having to see or catch them (Opdam and Müsgens 1976).

Processing chicks at the nest

Processing of the chicks at the nest was very similar to that of the adults, and was carried out at any time after they reached the age of 14 days. At this age there was no doubt about the sex of the chicks, and rings could be fitted without fear that they might

slip over the still developing foot. Although the chicks were weighed, and had a blood sample taken from them, no feather stamping (Section 1.3.3) was done. No linear measurements were made, and chicks were not fitted with transmitters.

Plate 1.5 Adult male and adult female Sparrowhawks illustrating size and colour differences. Both birds were marked with red patagial marks.

After processing, chicks were replaced in the nest and allowed to be reared to independence by their parents. At the time of ringing, all chicks were assumed to have fledged. In all years a search of the nest and the site post-fledging often revealed any late nestling mortality.

Processing data

Data were analysed using standard statistical tests (Snedecor and Cochran 1980; Sokal and Rohlf 1981; Fowler and Cohen 1983). Some statistical tests were run using Statview 512+ (BrainPower Inc.) and Cricketgraph (Cricket Software) software for the Apple Macintosh computer. Graphs were produced using Cricketgraph and an Apple computer. Maps were produced on an IBM computer using Windows, Scangal and

Paintbrush (Microsoft Inc.) programs and a Hewlett-Packard Scanjet scanner. Text was produced using Word (Microsoft Inc.).

Plate 1.6 Adult female breeding Sparrowhawk with red patagial mark (R). Antennaes for tail-mounted radio-transmitter (A) also visible.

In most cases, mean values presented in the text include a calculated error. Where the standard deviation is presented, this is indicated. Scientific names of the species named in the text are listed in Appendix 1 Table 1.1.

Chapter 2

Feeding Behaviour

2.1 Introduction

The food habits of many birds of prey are well known (Newton 1979), including those of the Sparrowhawk (Tinbergen 1946; Friemann 1967; Opdam 1975, 1978; Newton 1979, 1986). In general, in any particular locality, all species of birds within a certain range of sizes are preyed upon by Sparrowhawks. Tinbergen (1946) showed that Sparrowhawk predation can account for a large proportion of the annual mortality of some prey species. It has also been found that in certain situations, Sparrowhawks can significantly depress the populations of its prey, at least locally for short periods (Geer 1978).

Correlations have been made between food and aspects of Sparrowhawk ecology. For British Sparrowhawks, prey abundance/delivery rates have been related to the nesting density (Newton, Wiley, and Mearns 1986), the range size of breeders (Marquiss and Newton 1981), the date of egg laying (Newton and Marquiss 1981, 1982b, 1984), the size of the clutch (Newton and Marquiss 1981), and the growth rates of nestlings (Moss 1976, 1979).

Food is also related to moult, overwintering and perhaps dispersion in *Accipiter nisus* (Newton 1986). Feathers grown when food is scarce may display weakened places in the feather ('fault' or 'fret' marks). Food availability must certainly affect the choice of wintering area, and is probably the prime motivation for Sparrowhawk migration in other parts of the world. In Sparrowhawks, birds reared in upland (and therefore generally poorer) habitat dispersed farther (Newton 1986). These long-distance dispersers were less productive This close association between food and so many aspects of Sparrowhawk breeding biology indicates that reproductive success is dependent on a good supply of food.

Although the food habits of the Sparrowhawk have been studied thoroughly in rural areas, those of city Sparrowhawks have not been described. This chapter is based on

an investigation into the food availability and the diets of the urban Sparrowhawks in Edinburgh, and makes comparisons with studies elsewhere.

2.2 Methods

Prey abundance and the diet of Sparrowhawks in Edinburgh was examined from January to late July, 1986-1989. Estimates of prey abundance using point counts were made. In as much as was possible the methodology of the counts followed Newton *et al.* (1986), involving 10-minute counts of all the birds heard and seen within a 30 metre radius of the observer. For this analysis, counts were made between 1 May and 14 May of 1987 and 1988 during visits made to urban Sparrowhawk nesting places to determine occupancy. Some nesting places were visited more than once during early May. For each site between 1 and 6 visits, and between 1 and 14 counts were made per year. Counts were made at other times of the year, but were less rigorously undertaken, and are excluded from any analysis. However, they were useful in confirming (but not quantifying) the temporal variation in prey levels of certain species (particularly migrants), and different age classes.

All counts were made between 0600 hrs. and 0900 hrs., and only when it was not raining and when winds were not high. Mean counts were compared between nesting places and between years. Prey abundance may not have equated exactly with prey availability, but a detailed analysis of the susceptibility of prey species to Sparrowhawk predation was beyond the scope of this study.

Counts were made of all avian prey within the range of sizes (Goldcrest to Wood Pigeon) taken by the Sparrowhawks, but did not detail the species composition of the urban prey base. The mean number of prey-birds seen or heard on each territory was used as a rough measure of prey availability.

The flocking behaviour of some prey species (e.g. Starling, Pigeon, Redwing) was a possible source of bias in prey counts. Counts were conservative since large flocks (> 10 individuals) of prey species were excluded from the analysis. By not including the large flocks I think my counts better estimated the availablity of prey rather than the total numbers. Prey counts were made only in the places in the city where Sparrowhawks were known to nest (where there were trees), and may not have reflected the overall prey abundance in the city.

Sparrowhawks pluck their prey before eating it. To study diet, remains of kills made by the urban Sparrowhawks were examined. Collections of prey remains were compared to the avian skin collection at the National Museum of Scotland, and Brown, *et al.* (1987) for identification. A reference collection of the feathers of common prey species was made, and used to confirm the identity of prey remains in the field. Most prey could be identified to the species level. Age and sex of prey could sometimes be determined.

Prey species that could not be identified could usually be assigned to a size class: small (e.g. Chaffinches, Sparrows, and Tits), and medium-large (mostly Starling and Thrush species). Observed prey deliveries were only included in diet composition analysis except when when they could be positively identified.

Few kills were actually witnessed, and for much of the time during which prey collections were made, the female was not hunting. For this reason, no distinction could be made between kills made by male or female Sparrowhawks. A difference in the size of the prey taken by males and females has been shown by Opdam (1975). Also, kills made by adults and those made by yearlings could not be separated. Avian prey killed by other predators (Tawny Owls, Kestrels, cats, and foxes) were distinguishable from those made by Sparrowhawks. Tawny Owls plucked more than one feather at a time, so their prey remains were characterized by fragments of skin being still attached to the feather quills. Mammalian predators generally chewed the ends of the feathers of their prey.

Effort in prey-remains collection was concentrated around the nesting places during the springs and summers of 1986-1989. Some searches were made at other times of the year, but because Sparrowhawks were less tied to the nesting place, remains were more scattered at these times. Still, searches in the autumn and winter were important in that they revealed predation upon migratory species, and included kills by both males and females.

The amount of biomass each prey species contributed to the diet of the Sparrowhawks was calculated using the prey weights detailed by Opdam (1975,1978). The different weights of full-grown and fledgling individuals were taken into account when determining total biomass. Weights of the fledglings of some species were known from Opdam (1975, 1978). Where I was unsure of fledgling weight, I

estimated it to equal 60% of the adult weight. This estimation was probably most important in determining total biomass of the larger prey species.

Nesting places were classified subjectively as being 'urban', 'suburban' or 'rural'. Urban nesting places were usually small in terms of woodland area. They were located in built-up areas of the city (i.e. city gardens). Suburban nesting places were usually more extensively wooded, with fewer buildings (i.e. golf course). Rural sites were characterized by few buildings, and relatively large woodland areas. All rural sites were situated on the edge of the city study area.

2.3 Results

2.3.1 Prey counts

The mean number of prey species at different nesting places in Edinburgh ranged from 3.6 to 9.8 (N=208 counts). No significant difference between years was found. At the urban nesting places, mean prey counts (7.2 $\pm$ 0.6; N = 16 nests) were significantly higher than those in the rural areas (4.9 $\pm$1.4; N = 8 nests)(z-test; $P < 0.01$). The prey counts at suburban nesting places were intermediate, and averaged 5.4 $\pm$ 1.9 prey items/count (N = 6 nests).

Although unquantified some species were very plentiful. Large numbers of feral pigeons lived within the city, and concentrated around the city centre. House Sparrows and Starlings were also very numerous throughout the study area. Large numbers of migrants sometimes arrived in Edinburgh, then moved on. In 1986, large numbers (in comparison to other years of the study) of Redwing and Fieldfare passed through the city in the late winter-early spring. An assessment of the actual numbers of these migratory species was not made. These migratory species were also seen in Edinburgh during autumn in some years. I did not conduct surveys or search for prey remains at that time of year.

2.3.2 Food habits

A total of 1621 prey items were identified for the urban Sparrowhawks. Only one non-avian prey item was found, a small rodent (vole?). Thirty-four bird species were represented. A further 42 deliveries were witnessed of unidentified prey

species during the pre-nestling stages. Thirty-six of these unidentified items were classed as 'small' prey items, the others were Starling-sized or larger.

Table 2.1 lists the species found as prey items of Sparrowhawks in Edinburgh. House Sparrow (26.3), Chaffinch (17.4), Starling (13.5), and Blue Tit (11.5) were the only species which comprised over 10% of the diet of the urban Sparrowhawks.

Of the species which contributed more than 1% of prey items to the diet of Sparrowhawks, Fieldfare and Redwings were the only species to show significant variation in the number of kills found between years. Twenty-seven (77%) of the Redwing and 24 (77%) of the Fieldfare kills were found in the spring of 1986. Fieldfare and Redwing kills were ranked 6th and 8th in importance in terms of biomass (Table 2.2).

The size range (mass) of birds preyed upon by urban Sparrowhawks varied from Wren (< 8g) to Wood Pigeon (> 500g). See Table 2.1. There was no significant difference in the size of the prey taken by Sparrowhawks nesting in urban, suburban, and rural areas (Moss, 1976; Newton 1986; Newton et al. 1986) The percentage of biomass that each species contributed to the Sparrowhawk diet assumed that each kill was eaten completely.

Even though large prey, particularly feral pigeons, were plentiful in the city-centre territories, few very large prey items were taken there. Throughout the study area the kills of large prey were not always totally consumed by the Sparrowhawks. Of the 3 Wood- and 4 Feral Pigeon-kills found, only 1 Feral Pigeon was known to be eaten completely by Sparrowhawks. In the others, 1 Wood- and 1 Feral Pigeon were known to have been scavenged. The fates of the other 4 pigeon kills were unknown. The disappearance of these large prey items illustrates that the actual contribution to the diet of Sparrowhawks by these species is less than that calculated.

Two attacks by Sparrowhawks on feral pigeons were witnessed, both by adult females in March. In one the pigeon was killed and partially eaten, but disappeared over night. The other was caught, but escaped after a prolonged struggle, one in which the Sparrowhawk had actually started to feed. In both cases, the amount of time spent struggling and feeding was in excess of 25 minutes. All of this time was spent on the ground.

Table 2.1 Species found as prey items of Sparrowhawks in Edinburgh, 1986-1989.

Species	Occurrences	(%)	Biomass in grams	(%)
House Sparrow *Passer domesticus*	432	(26.7)	13,032	(22.4)
Chaffinch *Fringilla coelebs*	285	(17.6)	4,050	(6.9)
Starling *Sturnus vulgaris*	222	(13.7)	11,232	(19.3)
Blue Tit *Parus caeruleus*	188	(11.6)	1,502	(2.6)
Blackbird *Turdus merula*	96	(5.9)	8,113	(13.9)
Great Tit *Parus major*	69	(4.3)	1,249	(2.1)
Robin *Erithacus rebecula*	44	(2.7)	688	(1.2)
Mistle Thrush *Turdus viscivorous*	43	(2.6)	4,284	(7.4)
Dunnock *Prunella modularis*	42	(2.6)	792	(1.3)
Song Thrush *Turdus philomelos*	39	(2.4)	2,867	(4.9)
Redwing *Turdus iliacus*	35	(2.2)	2,100	(3.6)
Fieldfare *Turdus pilaris*	31	(1.9)	3,348	(5.7)
Coal Tit *Parus ater*	19	(1.2)	156	(0.3)
Greenfinch *Cardeulis chloris*	17	(1.0)	462	(0.8)
Goldfinch *Carduelis cardeulis*	9	(0.6)	162	(0.3)
Brambling *Fringilla montifringilla*	7	(0.4)	133	(0.2)
Tree Sparrow *Passer montanus*	5	(0.3)	85	(0.1)
Chiffchaff *Phylloscopus collybita*	5	(0.3)	20	(<0.1)
Feral Pigeon *Columba livia*	4	(0.25)	1,220	(2.1)
Budgeriegar *Melopsittacus undulatus*	4	(0.25)	~35	(<0.1)
Wood Pigeon *Columba palumbus*	3	(0.2)	1,270	(2.2)
Collared Dove *Streptopelia decaocto*	3	(0.2)	405	(0.7)
Bullfinch *Pyrrhula pyrrhula*	3	(0.2)	60	(0.1)
Goldcrest *Regulus regulus*	2	(0.1)	10	(<0.1)
Whitethroat *Sylvia communis*	2	(0.1)	18	(<0.1)
Willow Warbler *Phylloscopus trochilus*	2	(0.1)	14	(<0.1)
Blackcap *Sylvia atricappila*	2	(0.1)	33	(<0.1)
White Wagtail *Motacilla alba*	1	(0.06)	19	(<0.1)
Waxwing *Bombycilla garrulus*	1	(0.06)	~20	(<0.1)
Wren *Troglodytes troglodytes*	1	(0.06)	~7	(<0.1)
Woodcock *Scolopax rusticola*	1	(0.06)	300	(0.5)
Swift *Apus apus*	1	(0.06)	~17	(<0.1)
Cockatiel *Leotolophus sp.*	1	(0.06)	~110	(0.2)
Cockatoo *Kakatoë sp.*	1	(0.06)	~350	(0.6)
Small mammal (Bank vole?)	1	(0.06)	~27	(<0.1)
Total	1621		58190	

Feral pigeons were not the only prey items to be killed or eaten on the ground. Representatives of all prey size-groups were seen being eaten on the ground by Sparrowhawks, but in 11 of the 12 cases in which Sparrowhawk kills of small birds (Chaffinch size or smaller) were seen, the prey item was taken to a branch before being plucked (and consumed).

2.4 Discussion

Sparrowhawk feeding ecology had already been extensively studied (Tinbergen 1946; Friemann 1967; Opdam 1975, 1978; Newton 1976 a, 1986). Relatively little effort was put into investigating the diets of the urban population. Some biases existed in the data collected on prey availability and its utilization by Sparrowhawks in Edinburgh.

For example, more data were collected on the diets of established breeders than other birds, and data collection was concentrated at better quality nesting places. Since prey counts were made at the nesting places, the abundance of prey in the inter-nest areas was not directly assessed, but the importance of these areas as places to hunt was obvious since most kills were made away from the nesting place. This was known from both behavioural observations at the nest (Chapter 6) and radio-tracking (Chapter 4). No counts were made in the areas of the city where there was no nesting habitat (no trees).

In most instances prey counts were made in woodlands which were relatively small, so some open-country birds were recorded, but no counts were made in entirely open country. In other studies (Tinbergen 1946; Newton 1986), the proportion of food obtained by Sparrowhawks in non-wooded areas was lowest at this time of year, so the lack of data on open-country prey species in this study may not have been so important. On the other hand, the lack of large tracts of woodland in the city may have made prey species found in open areas more important for the urban population.

In some places human factors such as lawn mowing and gardening influenced both the ability to census prey species, and the collection of prey remains. Also, although most of the nesting places were checked regularly during the field season, some were checked less frequently than others due to difficulties with access or their remoteness from the centre of the study area. Weather and prey size have been noted as sources of further bias in the analysis of Sparrowhawk food habits by Newton (1986) and Tinbergen (1946).

The priority given to behavioural observations over the collection of other data in the spring-time affected both prey counts, and the collection of prey remains. Some nesting places were visited more often than others. At these nesting places pairs

were usually established early, and were usually reproductively successful. The effect this bias had on the mean number of potential prey items counted, and the number and composition of prey remains collected was unknown. Being 'high quality' territories, presumably the counts and number of kills would be generally higher.

The counts of potential Sparrowhawk prey species within Edinburgh show that prey is plentiful in the city. Although mostly within the range of prey numbers found by Newton *et al.* (1986) at other (rural) areas in Britain where Sparrowhawks nest, the counts made in the city centre of Edinburgh were particularly high. However, this assessment of prey numbers is subject to the biases discussed above, and might overestimate the actual numbers of prey available to the Sparrowhawks throughout the city.

This study shows that in general the feeding behaviour of the urban population is similar to that of the rural population --- the hawks feed upon whatever prey (within a particular size range) is present (Newton 1976, 1986: Opdam 1975, 1978). This characteristic is highlighted by the fact that exotic species such as the Budgeriegar were found as kills, but were not seen during prey counts. The appearance of migrants, and fledgelings in the diet before they were noticed in the area illustrates further that Sparrowhawks prey upon all potential items in the area.

In a more detailed study of the Sparrowhawk/prey relationship, Opdam (1978) examined the diet of Sparrowhawks which hunted farmyards and garden villages (the habitat-type in his study which most resembled that in the city). There, House Sparrows, Blue Tit, Great Tit, and Greenfinch all occurred in the diet more than would be expected from their abundance. Starling, Song Thrush, and Blackbird all occurred in the diet less than was expected. In that study, as in Edinburgh, the House Sparrow, Chaffinch and Blackbird were important Sparrowhawk prey species. As in that study, very few prey were small, secretive species (Wren, and Goldcrest).

The composition of the urban Sparrowhawk diet could have been influenced by a clumped distribution of certain prey species, such as House Sparrows. In his Dutch study, Opdam (1978) suggests that, in particular, the large populations of House Sparrows in cities might be a constant food resource which could be utilized by non-urban Sparrowhawks at times of low supply of prey in their habitat. At the time of that study Sparrowhawks wintered in urban areas, but were yet to breed there in any numbers. Such a response might result not only in a movement of individuals into

the city for the winter, but an increase in the number of rural-raised birds which come to breed in the city (See Chapter 3).

Although plentiful, large species, such as feral pigeons, are usually not taken by urban Sparrowhawks. Since the investigation into the diets of the Edinburgh Sparrowhawks centred on the spring and summer, when the male is doing much of the hunting, smaller prey would be expected. However, there might be other reasons for the dearth of larger prey in the diet. That the prey species of male Sparrowhawks are (on average) smaller than those of the females has been documented in other studies (Tinbergen 1946; Newton 1986; Opdam 1975, 1978). If this is true for the urban Sparrowhawks, the lack of large prey could be largely an effect of the biases toward the examination of breeding individuals and their nesting places. In this study, the relatively few large prey items delivered to the non-hunting female during the pre-nestling stage by the male Sparrowhawk suggests the same difference in mean prey size of male and female exists in the urban Sparrowhawks.

Because large prey is dangerous for the Sparrowhawk to attack, Newton (1986) suggests that large prey in the diet indicate hunger, due to poor hunting ability or poor habitat. Within the city, counts of potential prey (See above), and breeding data (Chapters 3 and 5) argue against either habitat or breeders being of low quality.

If a relatively large prey item is caught, Sparrowhawks usually pluck, kill, and feed on the ground. This was the case for the pigeon attacks witnessed in Edinburgh. With large prey which cannot be carried (Marquiss and Newton 1981), Sparrowhawks have been known to return to feed on them for a number of days (Newton 1986). In the rural areas, large kills which a Sparrowhawk could feed upon for a number of days may be less likely to remain undisturbed within the city. With people, cars, and numbers of potential predators (cats and dogs) about, Sparrowhawks within the city may be less willing to prey upon larger species, because of the time spent on the ground when these species are captured.

The structure of the urban habitat may also favour the predation of smaller species. The Sparrowhawk usually depends upon surprise to capture its prey (Newton 1986), the structure of urban areas with small clumps of trees and some areas devoid of vegetation may serve to both concentrate small woodland prey species, and make it more difficult to catch larger species that prefer open areas. The difference in the diets of Sparrowhawks in different, non-urban habitats suggest that some prey

species are more abundant/vulnerable in certain habitats than in others (Opdam 1978; Newton 1986). This study could not determine the relative vulnerability of the available prey species.

In Edinburgh, passage migrants might have been an important late-winter food source for the Sparrowhawks in certain years. This study was unable to assess the importance of the migrants because they only appeared in numbers in one of the years. The number of migrant kills found probably underestimates their importance. Passage migrants represented a fairly large proportion of the winter prey of Sparrowhawks in southern Scotland (Newton 1986), and in western Europe (Opdam 1978).

Migrants returning to breed in Edinburgh did not contribute significantly to the total biomass consumed by Sparrowhawks. In his study area, Opdam (1978) and Newton (1986) did not think breeding migrants were very important in the diet of Sparrowhawks, but emphasized the importance of a plentiful supply of sedentary prey species in Sparrowhawk reproductive success. However, the abundance of breeding migrants during the spring limits breeding in other raptors (e.g. Peregrine Falcon, Thiollay 1988; Cooper's Hawk, Snyder and Wiley 1976).

In conclusion, seasonal variation in the diet of Sparrowhawks, as well as the variation in their diets in different habitats has been examined elsewhere (Newton 1986; Newton and Marquiss 1981, 1982b; and Opdam 1978). Those studies conclude that shifts in Sparrowhawk diets reflect the abundance and vulnerability of particular prey species, and that any suitably-sized species, as long as it is plentiful, can be important to Sparrowhawks. Generally, the findings of my less detailed study in Edinburgh are consistent with those conclusions.

CHAPTER 3

Turnover, Movements, Population Size and Composition.

3.1 Introduction

In any Sparrowhawk population, the breeding sector is easily counted because breeders are tied to the nesting place for several weeks during the spring, but non-breeders cannot only be counted indirectly. In Sparrowhawks, nesting density has been used as a measure of population size in particular areas (Enemar and Unger 1977; Newton *et al.* 1977; Petty 1979; Bomholt 1981, Nilsson 1981), and Newton (1985) estimated the size of the non-breeding sector in one area from knowledge of the age of first breeding and annual survival.

Estimates of mortality rates derived from breeding-population composition, and recruitment and recovery rates of ringed birds have been used to provide details of Sparrowhawk demography (Newton 1975, 1986; Newton *et al.* 1983). Ringing also allows the movement of birds within the population to be studied, as well as immigration and emigration. Mortality, movement, turnover, and the age and sex composition of rural British Sparrowhawk populations have been investigated by Newton (1986); Newton and Marquiss (1982a, 1983); Newton *et al.* (1981); Newton *et al.* (1983); and Petty (1979).

This chapter investigates the size and structure of the Sparrowhawk population within Edinburgh. The density of breeding pairs, turnover of breeders, and age/sex ratios during the breeding season are examined, as is the site fidelity of ringed and colour marked birds. Causes of mortality among Sparrowhawks are discussed, and estimates are made of the survival/mortality rates of the different sexes and age classes.

3.2 Methods.

3.2.1 Sparrowhawk nesting density

As an index of population size, nesting densities were calculated. Two measures of Sparrowhawk nesting density were made: nearest-neighbour distance (between

nests) and the number of pairs per 100 km^2. These were chosen for their comparability with other studies, and were calculated for both actual and potential nesting places. Definitions of 'potential' and 'actual' nesting places are given in Chapter 1. Potential nesting places (sites) were where Sparrowhawks were known to have nested previously, actual nesting places were where they nested during that particular year. Since Sparrowhawks pairs do not typically nest within 300 m of one another(Newton 1986), all nesting places were treated as distinct.

3.2.2 Age and Sex Ratio

The age and sex composition of Sparrowhawk populations changes from season to season and from year to year (Newton 1986). The determination of these ratios for the Edinburgh population was confined to the breeding period.

Central to the examination of age and sex ratios was the capture and ringing of free-flying individuals, and the ringing of fledglings (Chapter 1). The capture of live birds by myself, and recovery of dead individuals by members of the public provided the data for the determination of population composition. Age was determined for both males and females using plumage characteristics, colour marks, and rings (Chapter 1). Because I was unable to catch all the breeding males, age was determined for some of these from plumage only, and early in the breeding season. Therefore, I could not be absolutely sure that some individuals were not identified at more than one nesting place.

The sexes of Sparrowhawks are separable by size and plumage (Cramp, *et al.* 1980). Sex ratio differences within the population could be caused by inequalities in mortality, immigration/emigration, or in the sex ratio at fledging (Newton 1986). An absolute determination of the sex ratio could not be made, but a basic investigation into the relative proportions of each sex within the population was made by examining the sex ratios of free-flying birds captured, and dead birds found by members of the public. Both of these ratios could however be biased.

3.2.3 Causes of mortality and estimates of survival

Causes of death in free-flying Sparrowhawks were examined. In many cases, no reason for mortality was obvious. For some corpses contaminant analysis was undertaken by the Institute of Terrestrial Ecology at Monk's Wood as part of a

monitoring scheme of pollutants in predatory birds. Methodology is described in Cooke *et al.* 1982. Although in Edinburgh, pollutants were not known to be a direct cause of death, the results of the analysis are presented here. Pesticide levels in eggs, and their effect on production are discussed in Chapter 5.

Yearling and adult survival estimates were made using the recovery ratios of different age groups and known age breeders. Recoveries of dead birds were not used to estimate age specific survival (See Lakhani and Newton 1983), but were used to supplement other evidence suggesting survival rate differences.

3.2.4 Turnover and recruitment

'Turnover' refers to the change, due to movement or mortality, of one or both of the occupants of a particular nesting place from one year to the next. Turnover was assessed during the breeding season. The plumage differences between yearling and adult and/or the ability to spot a ring or colour-mark sometimes made it more likely to identify individuals that were new to a site than to confirm that an individual was the same as in the previous year. On the other hand, the chances of recapturing individuals was higher among those that stayed than among those that moved, since some could move out of the study area. Information on females was most complete.

3.2.5 Movement

Three types of movement were recognized: (1) movement from the place where a bird was reared to the place where it bred, natal dispersal (Greenwood 1980) (2) movement from one breeding place to another in a different year, breeding dispersal (Greenwood 1980), and (3) movement between two places within the study area, only one of which is a nesting place. Comparisons were made between yearlings and adults, and between breeders and non-breeders. Too few males were recovered to make comparisons between the sexes.

3.3 Results

3.3.1 Sparrowhawk nesting density

Seventy-four potential nesting places were identified for breeding Sparrowhawks (Chapter 5). These were located in private and public gardens; golf courses; private

and public woodlands; cemeteries; the grounds of hospitals, schools, and businesses; and public walk-ways; as well as waste and temporarily idle ground.

Throughout the winter, October-February, the presence of prey remains indicated that all potential nesting places were used by Sparrowhawks. This was confirmed by tracking radio-marked birds (Chapter 4). Generally, in late February pairs began to establish themselves as breeders in some woodlands (although behaviours associated with breeding were observed in some places as early as November, Chapter 6).

Fifty-one (69% of potential sites) different actual nesting places were identified within the study area at least once during the study (See Chapter 5); 19.2 nesting places/100 km^2. The mean nearest-neighbour distance between actual nesting places was 0.95 $\pm$ 0.09 km (Range .25-4.2 km.).

In January and February of each year virtually all nesting places were frequented by at least one Sparrowhawk. Male and female individuals were seen together at nesting places, early in the season in 41 instances in 1986, in 45 instances in 1987, and in 46 instances in both 1988 and 1989. The nearest-neighbour distance between places where both male and female were seen early in the season was 1.1 $\pm$ 0.2 km, and the mean density was 17 nesting places/100 km^2.

Twenty-two (43%) nesting places were occupied (at least a nest structure was built, see Chapter 1) in 1986, 26 (51%) in 1987, 27 (53%) in 1988, and 27 (53%) in 1989, a mean of 9.6 occupied nesting places/100 km^2 (Chapter 5). The mean nearest-neighbour distance between occupied nesting places for all years was 1.3 $\pm$ 0.08 km (Table 3.1).

Table 3.1 Nearest-neighbour distances of occupied Sparrowhawk nesting places in Edinburgh, 1986-1989.

Year	N	Mean	S.D.
1986	22	1.36	0.94
1987	26	1.31	1.02
1988	27	1.39	1.04
1989	27	1.14	0.52

In 6 cases nesting places were less than 400 m apart. In each case, although there was no consistent difference in the age of the breeders, these were always separated

temporally, with one having eggs 7-10 days before the other. Too few instances of nesting places being extremely close together were found to test whether the temporal separation between them was different from the separation found between nesting places that were not close together. I could not be absolutely sure in all cases whether nesting sites situated close to one another represented distinct or alternate nesting places. Five actual nesting places were found only 300-500 m away from potential nesting places.

Although some nesting places were close to one another or situated in single trees rather than 'woodland' (Chapter 5), radio-tracking (Chapter 4) and behavioural studies (Chapter 6) often revealed these nests. I estimate a maximum of 2-3 nests were not found in a given year. Since radio-tracking was primarily done in the centre of the study area these undiscovered nesting places were most likely located on the fringes.

3.3.2 Population composition

The composition of the Sparrowhawk population was determined largely from ringing and identification of individuals from colour-marks. 91% of the known breeding females were captured or identified in the four years (Table 3.2), and 23% of the males.

Table 3.2 Proportion of breeding Sparrowhawks identified in different years in Edinburgh.

Year	No. of nests	No.(%) of hens identified	No. (%) of cocks identified
1986	22	17 (77.2)	4 (18.2)
1987	26	24 (92.3)	6 (23.1)
1988	27	26 (96.3)	6 (22.2)
1989	27	26 (96.3)	7 (25.9)
TOTAL	102	93 (91.2)	23(22.5)

3.3.2.1 Sex Ratio

3.3.2.1.1 Fledglings

Year to year production of male and female offspring by the breeding Sparrowhawks varied widely. In 1986 only half as many females were produced as males, and only

about 40% of the average female production for all other years. This notwithstanding, there was no significant difference between the production of males and females in in all years combined (Chapter 5, Table 5.1).

3.3.2.1.2 Non-breeding

The only hints to non-breeding sex ratios within the urban population comes from birds which in the winter (October-January), were caught live and known not to have bred, or been recovered dead. In the winter months, 9 males were caught and 5 females. Of the 30 ringed birds recovered dead by members of the public, 23 were females. This was not significantly different from expected.

Three male and four female breeders were lost late in the pre-nesting period from nesting places that were typically productive. I could not confirm whether some breeders were chased from their nesting place by their replacements. In two male and one female replacement incidents, the original breeder was known to have died before the replacement took place. In all these cases replacement was almost immediate, taking less than a week. This rapid replacement of breeders not only indicates that (at least in those years) neither male or female numbers limited the number of occupied sites, but implies breeding population limitation by territorial behaviour. Behavioural details of two of these replacements (one male and one female), and a discussion of Sparrowhawk territorial behaviour in general are given in Chapter 6.

3.3.2.2 Age ratio

Ages of birds trapped in the breeding season suggested that the age composition of the breeding population differed from that of the non-breeding population. The age ratio was investigated only for breeders, but inferences on the age ratio of non-breeders can be made through calculation of survival estimates (See later). Insufficient data were gathered to assess age ratios of non-breeders directly.

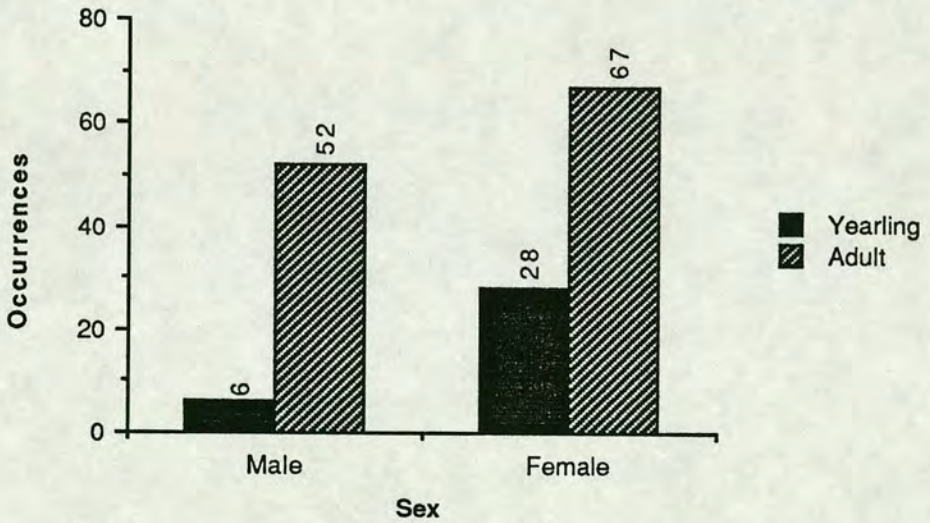
3.3.2.2.1 Age of breeders

In 55 cases the ages of both members of the breeding pair were determined, and in 40 cases just that of the female. Since most of the female breeders and all female fledglings were ringed during the study, the age structure of the breeding female

population could be examined more closely. The ringing data in 1989 are most illustrative of the specific age composition of the breeding female population. In that year, 9 females were breeding in their first possible breeding season (as yearlings), 3 in their second season, and five were in what was at least their second season. One bird was breeding in its third season of life, one in at least its third. Two females bred in their fourth season, one in at least its fourth. One female was known to have been breeding in her fifth season. No breeding females were breeding in 1989 that were over 5 years old. In all years combined, of known-age breeders, 67 adult (70.5%), and 28 (29.5%) yearling females attempted to breed. The oldest, known-age, breeding female was 5, but in such a short study, it was impossible to record older birds.

The age of 58 breeding males was determined: 6 (10.3%) were yearlings, 52 (89.7%) were adults (Figure 3.1). The oldest breeding male of known age was 5.

Figure 3.1 Age classes of breeding Sparrowhawks in Edinburgh, 1986-1989.



3.3.2.3 Causes of mortality and survival rates

Twenty-eight Sparrowhawks were found dead, 21 in their first year, and 7 in later years. Twenty were females. There was no difference in causes of death between the two age classes, or the sexes, with the majority (18) dying after colliding with some man-made object: wires, windows, or cars. Two were shot, and one died of starvation after being caught in a building. Seven died of unknown causes. One un-ringed, adult female was found decapitated, suggesting predation.

Complete results of pesticide analysis carried out on Sparrowhawks found in Edinburgh are presented in Appendix Table 3.1. Livers of dead Sparrowhawks that were analysed contained between 0.29 and 10.24 parts per million, wet weight DDE; between 0.20 and 2.31 ppm dieldrin; between 0.67 and 28.42 ppm PCB's; and between 0.00 and 4.36 ppm of Mercury. Only two corpses contained HCB of 0.07 and 0.09 ppm. these are below lethal levels (Newton 1979).

Four of the specimens were not from Edinburgh city, but the surrounding area. The pollutant levels fell within the range of those from within the study area, except for a yearling male (Ref. no. 8535) which was found shot in Fife, north of the city. The amount of DDE found in this bird was the highest of all the analysed specimens, five times as much as in the next most DDE-contaminated individual, but still insufficient to cause death.

The highest levels of dieldrin (2.31 ppm), and mercury (4.36 ppm) and the highest level of DDE (8.68 ppm) in a city bird were found in an adult female (Ref. no. 8861) for which no reproductive history was known. She was found in an intensively gardened area in the middle of the city.

The highest level of PCB's was found in an adult male (Ref. no. 9171L), from a city cemetery. This level was significantly higher than found in the other corpses (Dixon's Test for Outliers, $r_{21} = 0.856$, $a < 0.01$) The bird died in April, and at the time was holding a territory and attempting to breed.

3.3.2.3.1 Adult survival

Although sample sizes were small, a table of the ratios of known age, female breeders in each year was generated (Table 3.3). Pooling the adult ages 2-5 in all years the annual adult female survival is estimated at 53.3% (47% mortality).

3.3.2.3.2 Yearling survival

Yearling survival could only be approximated in females, using the equation:

$$\text{First year birds/Second year birds} = S_1(1-S_2)/(1-S_1)$$

(Newton, *et al.* 1983), where S_1 is the first year survival and S_2 is the annual survival in years beyond the first. Thus yearling female survival was calculated to be 40.7% (59% mortality).

Table 3.3 Age ratios of breeding female Sparrowhawks trapped in Edinburgh, 1986-1989 (Used to estimate the survival of adults (>1 year old) from the re-traps of breeders).

	Ratio between age groups			
Year	1:2	2:3	3:4	4:5
1986	4:3	3:-	- - -	- - -
1987	4:4	4:2	2:-	- - -
1988	8:0	0:2	2:1	1:-
1989	9:1	1:1	1:1	1:1
Total	25:8	8:5	5:2	2:1

3.3.3 Turnover of territorial occupants

In 70 cases the female, and in 18 cases the male of the breeding pair (N=102) was identified on a nesting site in successive years. Forty-three (61.4%) of the females, and 9 (50.0%) of the males present in the first year had changed in the second year, resulting in an average residency on a particular territory of only 1.4 years for the females, and 1.5 years for the males. There was no obvious difference in the turnover rate between years.

The turnover observed was not entirely due to mortality. Movement between nesting places also occurred. Where individual females were identified in successive years, 13 (30% of all female turnover) had survived and shifted to different territories a mean of 1.97 $\pm$ 0.49 km away. Also, three out of five females which probably skipped a year between breeding attempts, occupied new nesting places. No females were found to be breeding after a non-breeding interval of 2 years.

In 5 out of 14 (36%) cases where a male was known to have bred in successive years, he had changed territories. In 3 cases in which both breeders of a pair were identified and had moved territories in successive years, none showed mate fidelity.

In 23 (26%) instances, turnover (both male and female) was followed by the

occupancy of the territory by a yearling, and in 65 instances by an adult breeder.

3.3.4 Recruitment and age of first breeding

228 Sparrowhawks were rung as fledglings (119 males, 109 females (Chapter 5)). Of these, 7 females and 3 males were later identified as breeders in the study area. Among hens found breeding for the first time within the study area (1987-1989; N=31), 64% were in their first year, 13% were in their second year, and 23% were older than two. Too few males were caught as breeders to compare the difference in the rate of recruitment between the sexes

In 1989 (after 3 years of ringing most of the female breeders, and fledglings), 53.8% of all breeders trapped were new recruits to the nesting population (N=26), only 2 were ringed as fledglings in the study area. In that year at 20 nests where males were examined for rings, 13 were un-ringed either through capture as free-flyers, or recruitment from nestlings raised within the study area. There was no evidence that the rates of recruitment (either from the city-reared or general fledgling populations) were different for the sexes.

3.3.5 Movement

Sixty birds were caught and ringed as free-flying individuals (year-round). Twenty-three were initially caught as yearlings, and 37 were in adult plumage when first encountered. All nestlings were ringed (See Chapter 5).

Sixty-one ringed individuals were recovered later. Twenty-eight were found dead; 33 were encountered alive. The average distance moved between ringing site and recovery site was 6.7 $\pm$ 1.6 km (Range 0.0 - 51.0 km, Median 6.0 km), although surely this was biased against birds which moved long distances. Excluding the birds which made no move from ringing site to recovery site, only 4 moved away from the city centre (N=46).

Of the birds found dead, including 3 un-ringed individuals, more females than males were recovered (24:7). Of these, 23 were yearlings and 8 were older. No estimate of lifetime recovery rates could be made for either sex. See: Table 3.4

Table 3.4 Age of sex of Sparrowhawks recovered dead in Edinburgh, 1986-1989.

	Males	Females	Total
Yearlings	19	4	23
Adults	5	3	8
Total	24	7	31

Birds which were ringed as nestlings and recovered dead travelled a mean of 7.1 ± 1.7 km (N=20). In addition, four were recovered on their natal site shortly after fledging. Too few males were recovered to compare movements with those of the females.

Live recoveries were made of breeders (20), wintering individuals (11), recent fledglings (2), and birds which were found sick or injured, nursed back to 'health', and released (2). Two individuals recovered had been ringed by other ringers, one outwith, and one within the study area. The mean distance of recovery for live birds was 3.29 ± 0.79 km. Ten individuals were caught three times, only one of them was not breeding at the time of the third encounter. The ringed immigrant was one of these; it was caught as a breeder on three different, adjacent territories.

Nestlings ringed during the study were recovered both as breeders and non-breeders. Of male nestlings, 2.5% were recovered breeding; as were 6.5% of the female nestlings. 17.6% of the females ringed as chicks were caught as non-breeding yearlings (Table 3.4).

Table 3.5 Recovery of Sparrowhawks ringed as nestlings in Edinburgh,1986-1989. (Non-breeders could be determined by colour marks.)

Males		
Number of chicks ringed	119	
Recovered as non-breeder	5 (4.2%) in 1st yr.	1 (0.8%)in 3rd yr.
Recovered as breeder	3 (2.5%)	
Females		
Number of chicks ringed	109	
Recovered as non-breeder	19 (17.6%) in 1st yr.	1 (0.9%) in 3rd yr.
Recovered as breeder	7 (6.5%)	

There was no difference in the movement of birds ringed as nestlings and those ringed and recaught as free-flyers. Ringed, nestling females which later bred in the study area (N=6) traveled a mean of 3.3 $\pm$ 0.86 km from natal to breeding area. This distance equated to 3-4 territories, but was undoubtedly biased against birds which moved farther afield to breed. One female, ringed as a nestling outside the study area traveled 51.0 km to breed within Edinburgh. Including that individual, the mean was 6.1 km. Too few males were trapped that had been recruited from the study area to calculate their mean natal dispersal distance.

3.4 Discussion

Compared to other raptors in Britain, the size of the Sparrowhawk population, at 3000 pairs, is second only to that of the Kestrel (Newton 1986). Certain habitats are more productive than others, in terms of both nesting place occupancy and success (Newton *et al.* 1979, Newton 1986, 1988b). In the rural area, in suitable woodland Sparrowhawk nesting places were regularly spaced, and became further apart as altitude increased and land productivity decreased (Newton *et al.* 1979), and prey densities declined (Newton *et al.* 1986). Newton (In press) further suggests that the regulation of breeding numbers is determined to some extent by spatial variation in habitat quality. These same studies also indicate that breeder quality has an influence on occupancy (Chapter 5).

Urban Sparrowhawk population size and composition was difficult to determine given the differential rate of capture of males and females, and their secretive nature. Particularly within the city, biases existed in trapping since baited traps could not be left for long periods during the daylight hours, and were set more often in habitat favoured by the male when hunting (See: Opdam 1975; Marquiss and Newton 1982).

The nearest-neighbour distance found in Edinburgh was similar to those found in low-mid altitude sites studied by Newton *et al.* (1979). Prey densities were variable (Chapter 2), and may have played some part in determining the inter-nest spacing and nest site choice as in other studies (Newton *et al.* 1986, also see: Tilghman 1987 and Gilbert 1989). The Edinburgh nearest-neighbour distance was greater than the 0.82 kms that separated the Kielder Forest Sparrowhawks (Petty 1979). However, in Kielder, the nesting habitat for Sparrowhawks was not as fragmented as in the city. In all, the wider spacing of Sparrowhawks in Edinburgh

can probably be explained by differences in the availability of suitable nesting places rather than levels of prey, altitude, or land productivity. The intolerance of individual breeding Sparrowhawks to close neighbours could also be a factor (Chapter 6).

Within the city, the density of occupied nests per 100 km^2 was quite low. This is probably due both the high amount of land made unsuitable for nesting within the city, and the fragmented nature of the suitable woodland. In general, larger study areas (>100 km^2) such as Edinburgh tend to have lower densities, because they usually have greater amounts of unsuitable habitat. Newton *et al.* (1979) and Newton (1986) provide Sparrowhawk nesting densities from Britain and northwestern Europe for comparison; the nesting density of Sparrowhawks in Edinburgh is within the range of densities found elsewhere.

The rapid successful replacement of breeders removed from the population early in the breeding season, and the gaps in the map of the territories within the city indicated that within Edinburgh, the availability of suitable nesting places limited to some extent the number of breeding pairs. The fact that some sites which had been used in the past went unused during the study may have indicated a decline in the quality of nesting places.

More potential nesting places were frequented by Sparrowhawks in January and February than were actually occupied later in the spring. There were always 'floaters' in the population so mortality could not explain this discrepancy. The abandonment of these places could have been due to either low habitat quality and/or low breeder quality. Habitat quality was probably more important. When breeding places (at perennially successful nesting places) became vacant due to mortality late in the season, replacements were recruited very quickly.

Statistics relating to the age and sex composition of the urban population are not conclusively different from those of Newton (1986). He suggests that non-breeders comprise some 43% of the female population, a proportion which varies from season to season, and year to year. This large, unassessed pool of Sparrowhawks, trapping biases due to habitat partitioning by the sexes, and the possible greater rate of recovery of the larger females makes precise determination of the age and sex ratios in this short study impractical. Age and sex ratios could be influenced by differences in mortality, immigration/emigration rates, and the number of fledglings of each sex

produced. The sex ratio of nestling Sparrowhawks was unity, as found elsewhere by Newton and Marquiss (1979), and Gedeon (1983). The high proportion of unringed males observed in the breeding population may suggest high male mortality within the city, and a high recruitment of immigrants. This view is supported if the ratio of males that were known to move nesting places and survive to males which turned over, but were not known to survive was a true representation of adult male survival. Calculations by Newton *et al.* (1983) suggest that male mortality is greater than female mortality. In this study, examination of birds found dead may suggest female mortality is higher than that of males, although their rate of recovery might be higher than for males.

Many species of raptor have a relatively high mortality in the first year of life (Newton 1975, 1984; Newton *et al.* 1983; Rothery 1984; Saurola 1976; Henny and Wight 1972), the extent of which is inversely related to the weight of the species (Newton 1979). In Sparrowhawks, Newton *et al.* (1983) have estimated the mortality of the males to be greater than that of females (particularly in the first year). Male mortality rate could not be estimated in this study, but female mortality was high. The females' preference for hunting habitat (Opdam 1975; Marquiss and Newton 1982) which is more open than that of the male, may have made them more likely to be found by people, or more susceptible to the dangers of the city: cars, wires, and buildings. This could not be tested.

The yearling survival estimates of females in Edinburgh was lower than that of Newton *et al.* (1983). Annual variations in yearling/adult ratios have been found in other raptor species, and Mearns and Newton (1984) warn against determinations made over the short term. Adult female survival in Edinburgh was lower than that calculated by Newton *et al.* (1983).

The estimate of adult survival were lower than stable, declining, and increasing rural populations examined by Wyllie and Newton (In press) and Newton and Marquiss (1986). Comparing with those same studies, the percentage of breeding male yearlings was lower in the Edinburgh population in all those populations. For breeding females in Edinburgh, the proportion of yearlings was similar to that in the increasing population, but higher than the stable and decreasing populations. The percentage of yearlings in the breeding urban population was also higher than that found by Petty (1979).

The range of reported causes of Sparrowhawk mortality within the city were significantly dissimilar to those in rural areas (Newton 1986). Collision with man-made obstacles was the most commonly reported cause of accidental death, and more common than found by Newton (1986). This is probably because there are both more man-made obstacles, and because accidents might be more likely to be reported in the city. Although there were no cases where poisoning was known to cause mortality, the highest levels of pollutants were found in corpses in intensively managed garden areas in the middle of the city. The levels of DDE were low enough to be within the range of 'background' levels. The effect of PCB's on birds is less well known, but the outstanding level of 28.42 ppm is considered high (Prestt, *et al.* 1970).

Turnover within the city population was high, and similar to that found in low grade territories in southern Scotland. Comparing with all grades of territories, the urban Sparrowhawks displayed a slightly lower male turnover, and a slightly higher female turnover (Newton and Marquiss 1982a). In southern Scotland, turnover was most frequent among hens which had either failed, were yearlings, or had occupied poor territories in the previous year. Too few instances of turnover for each age class and of different production levels were observed to make a detailed analysis in the city. Nesting place quality could only be defined in terms of production, and no measurement taken at these places was clearly associated with lowered production (Chapter 5).

No mate fidelity in birds which shifted territories was observed, consistent with Newton and Marquiss (1982 a). As in other Sparrowhawk populations (Newton 1986), in territories within the city young stay for 3-4 further weeks after fledging (See Chapter 4), and over winter mortality and recruitment force a re-mixing of the breeders each spring. I would expect that a longer study would reveal some pairs which moved, but remained together in successive years given the pattern of movement to better quality nesting places, and the preference of adults to breed with other adults. This was not shown here.

In southern Scotland recruitment was an important factor in determining the year to year changes in nest numbers, with the percentage of previous breeders varying with spring weather (Newton 1986). Wyllie and Newton (In press) have shown recruitment to be lowest in a declining population, higher in a stable one, and higher still in one that is expanding. Recruitment, and in particular, number of yearling

females in the urban breeding population was high, and probably indicated a high adult mortality rather than an expanding breeding population since nest numbers were stable throughout the study (Chapter 5), and nesting places were probably limited.

Movements, whether local or long distance, are an important way in which animals react to change in food supplies. Batten (1972) showed that suburban gardens support the highest densities of breeding birds of any habitat in Britain. Edinburgh is characterized by woodland areas incorporated in an urban setting (Chapter 1) where high levels of potential prey are found (Chapter 2). It is possible that Sparrowhawks raised in rural habitat move in to over-winter and to breed, taking advantage of the high prey densities, while others move out of the city. There is no evidence for net immigration.

The distances traveled by both breeders and non-breeders were similar to those of Sparrowhawks throughout Britain (Newton 1975), with the distance of most shifts being less than 10 km. The smallness of the study area constrained the possible distances (as well as the time) of recovery, although the immigration of a bird from over 50 km away indicated that relatively long dispersals do occur. An expansion of the study area would be useful to better quantify not only the dispersal distances, but also the flow of rural recruits into the urban population.

Natal recoveries were also in line with other studies (Newton and Marquiss 1983). In that study, movements were related to breeding success, and the distance traveled by brood-mates was highly correlated The Edinburgh study was too short for such determinations.

In conclusion, the findings on the turnover, movements, size and composition of the urban Sparrowhawk population were similar to those elsewhere. Some of the findings of those longer studies are indicated in Edinburgh, but could not be proven given the shortness of the study, the small population size and a limited variety of habitat. The difficulty in capturing large numbers of breeding males limited any further illumination of their demography, as it has in other studies.

CHAPTER 4

Range and Roosting Behaviours

4.1 Introduction

Radio-telemetry has been used to study the ranging behaviour of many raptors, including Sparrowhawks (Newton 1979,1986), and is necessary to investigate certain aspects of their ecology (Kenward 1985). In birds of prey, range sizes vary, as does the extent of overlap between neighbours. In some raptor species ranges are almost mutually exclusive (e.g. Black Eagle, Gargett 1975), while in other species ranges overlap almost completely apart from the nest site (e.g. Eleonora's Falcon, Walter 1979).

For Sparrowhawk, ranging behaviour has been investigated in a southern Scottish, rural population by Marquiss and Newton (1981,1982). These ranges overlapped to some extent throughout the year, and varied in size with the social status, sex and age of the individual. In the spring, the the ranges of neighbouring breeding males were almost mutually exclusive, and varied in extent, according to prey densities (Marquiss and Newton 1982, Newton 1986).

Within their range, individual raptors establish night-time roosts. The position of these roosts is determined to some extent by security, and proximity to the nest (Newton 1976a). The use of different roosts can be affected by factors such as weather, competition for roosting sites, and human disturbance (e.g. Cebellos and Donázar 1990). Among raptors, roosting behaviours vary. Some species roost communally (e.g. Bald Eagle, and Egyptian Vulture), while others are solitarily roosters (e.g. Peregrine Falcon, Golden Eagle, and Sparrowhawk).

This chapter uses radio-telemetry and the identification of individual, colour-marked Sparrowhawks to investigate ranging and night-time roosting behaviour in winter and spring, and early breeding season association with nesting places. Most data were from birds which established pair-bonds early in the year and went on to breed successfully, or from non-breeders that did not form even temporary pairs. In one case though, a radio-marked, initially non-breeding yearling male replaced

an established adult breeder late in the season after the adult had died. The roosting and ranging behaviour of this individual is also presented.

4.2 Methods

To facilitate individual identification of birds which were observed as part of an investigation of breeding behaviours (Chapter 6), 19 Sparrowhawks were captured, ringed and colour-marked (Chapter 1), and fitted with a radio transmitter: 12 in the late winter-spring (January-May), and another 7 in the autumn and early winter (October-December). Some of the individuals from both seasons bred in the spring-time following radio-monitoring.

Appendix 2, Figure 4.2 illustrates the area in which all the radio-transmittered birds were caught, and in which most of the ranges of those birds were wholly contained. This area was chosen since it was relatively densely populated with territories which were usually successful, and the habitat was more consistently 'urban'. Terminology is defined in Chapter 1.

4.2.1 Radio equipment

The transmitters (SR-1; Biotrack, Wareham, U.K.), were similar to those used by Marquiss and Newton (1982). The transmitter was powered by a 1.35 volt mercury battery which provided a signal at 173 MHz for a maximum of 80 days (Appendix 1, Table 4.1). The transmitter and battery were fitted with main and ground-plane antennae, and potted in epoxy resin. Transmitters were assembled prior to trapping, but leads between battery and transmitter were left unconnected until a bird was caught. Radio packages weighed 5-6 grammes.

After the capture and usual processing of a bird (Chapter 1), transmitters were attached to the base of the two central rectrices (Kenward 1978, Marquiss and Newton 1982). The leads between battery and transmitter were connected, then water-proofed using quick-setting epoxy resin. All transmitters were tested prior to mounting, and frequencies were chosen to avoid confusion in identification of birds ranging in the same area. The main aerial was tied to one of the rectrices, the ground-plane aerial ran anteriorly, unattached along the back. Maximum length of tag attachment depended on moult or the durability of the cotton thread used in mounting the tag.

Radio-tracked birds were also fitted with colour-marks (Chapter 1). This was not so important in the determination of range, but confirmed the association of previously radio-tagged birds with certain territories.

The transmitter signal was picked up on an LA 12 receiver (AVM Electronics, Champaign, Illinois, U.S.A.), using a hand held three element yagi antennae (Mariner Radar, Lowestoft, U.K.). Headphones with volume control were used to amplify the signal, and exclude wind and city noises.

In ideal conditions (a clear day, with a radio-tagged bird soaring above the buildings), signals could be heard over 5 km away. Buildings and the topography of the city sometimes acted as shields and reflectors of the signals, so close quarter confirmation of a bird's whereabouts was imperative. No matter where the birds were, the many hills of Edinburgh allowed me to locate birds from a distance, and then find them more precisely at close quarters by triangulation.

4.2.2 Data collection and analysis

Since the main purpose of the radio-tagging was to aid in the behavioural studies, data were collected in a manner not ideal for the analysis of ranging behaviour. For some birds radio-fixes were made periodically, while others were under continuous surveillance. Although some birds were being radio-monitored continuously, The data points used in range size analysis were chosen to ensure spatial independence (Swihart and Slade 1985).

As far as possible, all birds were located in the early morning (usually before they had left the roost), 5-10 times during the day, and at night.

Although most tags lasted longer than the 4-5 days required to define the range at a particular season (Marquiss and Newton 1981), I could not predict their durability. So, after attachment of a radio-tag, I spent the next 4-5 days intensively following the newly marked individual. All ranges in this study were determined using a minimum of 46 fixes taken over 4-81 days (Appendix 1, Table 4.1). The variation in the number of days over which birds were monitored was due to the loss or failure of some transmitters, the death of some birds, and the abandonment of tracking due to egg-laying and incubation.

Sparrowhawks were tagged during two times of the year: 'winter' (October-December) and 'spring' (January-May). Sparrowhawk ranges change throughout the year (Marquiss and Newton 1982). In the spring, range changes were examined in certain individuals whose transmitter life spanned the changes.

Graphical analysis of Sparrowhawk ranges is limited in its ability to portray their dynamic nature, and at the same time focus on a definable physiological/reproductive state. Recognizing this limitation, analysis was undertaken with particular attention being paid to the comparability between and within sexes, years, age classes, and breeding status. Ranges were described using the maximum polygon area (mpa), in which the boundaries of the range connected the outermost radio-locations of an individual bird. This method was best for the purposes of this study, since detailed habitat analysis could not be undertaken in the allotted time. Some parts of the range were used more than others.

Because the size of raptor ranges varies with season (Newton 1976), it is desirable to collect radio data when the range size is not fluctuating. Data on early winter range size was gathered over a limited number of days to avoid the effect of changing range size. In the early winter, ranges were probably getting larger as prey became more scarce, so representations of range are probably less than or equal to the maximum range size in that year. Ages, and any breeding attempt in the following spring were noted.

In the spring, ranges were divided according to whether the bird bred in that year. It was difficult to ensure that the ranges determined represented those of birds in similar reproductive states. It is assumed that the ranges of established breeders in the spring, before breeding, were broadly comparable. Appendix 2, Figures 4.3-4.21 are range maps for all radio-tracked birds; other behaviours displayed by Sparrowhawks during the breeding season are examined in Chapter 6.

For breeders, roosting behaviour was examined in relation to egg-date. The behaviours of some birds were observed as they entered and left the roost site. Associations were also examined between where a bird roosted, and where the bulk of its day-time activities occurred.

No detailed analysis of Sparrowhawk habitat use within the city was made. It is hoped that the habitat within the city can be examined in retrospect and that ranging behaviour can be analysed in the light of that data at some point in the future. The importance of woodland to Sparrowhawks has been demonstrated by Newton and Marquiss (1982b).

4.3 Results

Nineteen Sparrowhawks were fitted with radio-tags in the winters of 1986-7, 1987-8, and 1988-9, and the springs of 1987 and 88. They included eight yearling, and 6 adult males, and three yearling, and 2 adult females. Males were probably more easily caught in the spring because the breeders were not only feeding themselves, but had increasing responsibility for the provision of food for the breeding females; also traps were generally set in areas probably preferred by males for hunting (See: Marquiss and Newton 1982). The tracking period averaged 53 days.

4.3.1 Roosting behaviour

4.3.1.1 General

Night-time roosts were generally in fairly dense, evergreen trees (e.g. Pine, *Pinus* sp., and Holly *Ilex* sp.), although as leaves appeared in the spring, deciduous trees were also used. The woodland surrounding the roost tree was more variable. Sparrowhawks roosted in large and small woods. Woodland composition was varied, and included wholly coniferous, mixed, and mostly broad-leaved stands. The distance to human disturbance, and the level of that disturbance varied as greatly as the nesting places (Chapter 5).

The roosting behaviour of the urban Sparrowhawks did not seem to be affected by the presence of Tawny Owls or Kestrels. In the larger woodlands, Sparrowhawks and Kestrels would avoid each other during the day time, but at night their roosts were sometimes very close (< 50m apart). Tawny Owls and Sparrowhawks shared the same nesting areas. These areas were not avoided by the roosting Sparrowhawks. The places where Sparrowhawks nested and roosted, but Tawny Owls did not, were all small isolated gardens/woodlands.

Individuals had a principal roost, and a variable number of secondary roosts. The principal roost was used most often, but when bad weather, or fading light caught the bird away from it, a secondary site was used. The principal roost sites sometimes changed, particularly if a Sparrowhawk attempted to breed at a place away from the roosting site. Principal roosts of all radio-tagged birds are shown on the ranges in Appendix 2.

Using colour- as well as radio-marks I was able to observe 17 instances (3 males and 14 females) in which birds that were known to have nested in two consecutive years roosted on the nesting place they had used in the first year. In 12 cases(2 males, 10 females) the birds that roosted on a nesting place in the late winter-early spring went on to breed there. The high number of females observed roosting on their nest site does not necessarily mean that more females than males actually roosted on their nest site, as it may have been an artefact of more females being caught and colour-marked.

It was difficult to quantify the process of secondary roost site selection, because the locations of these were not static. Perhaps the motivation for using secondary roost sites were different for birds in different reproductive states.

4.3.1.2 Winter-early spring

During the winter and early spring individuals sometimes spent a large proportion of the day at the principal night-time roost. The position of day-time roosts seemed to depend on a number of factors, including weather conditions and hunting success. For unestablished individuals, the location of a day-time roost might be dependent on where it had roosted the previous night. Whether an individual was associated with a place for reproductive reasons might also have affected day-time roost location. Chapter 6 discusses spring nesting-place attendance rates by breeding Sparrowhawks, and intrusion onto these places by other Sparrowhawks.

During the winter the mean number of roosting sites used by yearlings (5.1 $\pm$ 1.1 roost sites/10 nights of observation; N= 163 nights) was not significantly different from that of adults (4.5 $\pm$ 0.9 roost sites/10 nights; N= 82 nights)(F-test,v_1=15,v_2=7, F=3.51). See Table 4.1.

All the individuals radio-tagged in the winter which did not breed (N=3) were yearlings, and most of the breeders (N=4) were adults, so the comparison between breeders and non-breeders was similar to that between adults and yearlings.

Table 4.1 Use of primary and secondary roost sites by Sparrowhawks in the winter and early spring in Edinburgh 1886-1989.

	Number of nights (%) at roost	
	Principal	Secondary
Age of bird		
Adult	84 (52)	79 (48)
Yearling	45 (55)	37 (45)

Aggressive displays toward intruding Sparrowhawks during the winter were witnessed on only 5 occasions. Four were directed toward intruders of the same sex, in one an adult female drove off an adult male

In 4 of the intrusions the identity of the aggressor was known. Three (1 female, 2 males) of the four intruders went on to breed, 2 (1 female, 1 male) on neighbouring nesting places. The fate of the other was unknown. In all cases, the defending individual went on to breed at the site of the aggressive encounter. Since some residents roosted away from the nesting place (Section 4.3.1.3.1), and in early spring the amount of time spent on the nesting place by the resident Sparrowhawks was less than it was later on (Chapter 6), aggressive interactions at this time of year were fewer than later in the pre-egg time of year.

4.3.1.3 Spring

4.3.1.3.1 Breeders

Two types of roosting behaviour were observed in breeding Sparrowhawks of both sexes in the spring. Some birds, 'home-roosters', had their principal roost where they were attempting to breed (Examples: Appendix 2, Figures 4.7, 4.8, and 4.9). Others, 'remote-roosters', roosted principally in places (sometimes the nesting places of other Sparrowhawks) which were distant from their nesting place. The

roosts of some remote-roosters were almost 2km away and separated from the nesting place by up to 3 territories (Examples: Appendix 2, Figures 4.3 (a), 4.4 (b), 4.5 (a) and (c), and 4.6).

Two home-roosting adult males (Appendix 2, Figures 4.7 and 4.8) monitored up to the time of egg laying, roosted at a secondary site 13% of the time (N=79). There was no indication that there existed preferred secondary roosting sites for these normally home-roosting individuals. One bird spent 4 nights away from its principal roost, at 3 different locations, the other used 4 locations in the 6 nights it spent away from its principal roost. All cases of home-roosting males roosting at a secondary site occurred more than 2 weeks prior to the day on which the first egg was laid by the females with which they were breeding. In each case they spent only one night away from the nesting/principal roosting place. Later, they spent every night near their nests. I had no information on the roosting behaviours of breeding yearling males.

Secondary sites were not as well defined as the principal roost sites, and as in winter, wet weather or coming darkness seemed to be some motivation to roost at a secondary site. Sometimes these secondary roost sites were the nesting places for other Sparrowhawks. Although in at least 4 cases resident male breeders were known to be roosting at the nesting place when at the same time it was being used as a secondary roost by another male. No interactions between breeder and intruder were seen. The only home-roosting female which was radio-marked in the spring roosted at the nesting place every night she was observed (N=56).

Remote roosting was known for 8 individuals, only 4 (3 males, 1 female) were radio-tagged (Appendix 2, Figures 4.3-4.6). The proportion of nights that remote roosters spent at their principal roost prior to roosting at the nesting place varied. One male spent nights (N=16) only on the remote, primary roost site before moving to roost exclusively at the nest site. Over the 20 days just prior to egg laying, another male spent 8 days at the remote, primary site, then 3 days at a secondary site in between the remote roost and the nest, and then 4 days back at the remote roost, before making the nesting place his roost site. Table 4. 2 summarizes the roosting behaviour of radio-tagged Sparrowhawks in the spring

The mean distance from nesting place to remote roosting site of radio-tagged birds was 1.7 km. Some birds had to by-pass at least one nesting place during the trip to

and from their principal roosting place. In some cases the roost site increased the size of the range (Section 4.3.4 and Appendix 2, Figures 4.3, 4.4, and 4.5).

In 2 of 4 cases of remote-roosting, male breeders attempted to breed in two consecutive years in the same places (Appendix 2, Figures 4.4, 4.5). In both, the nesting place was the principal roosting site for their mates. The nesting place of another remotely nesting male breeder was being used as a roosting site by yet another male Sparrowhawk. Whether either of these birds had previous breeding experience at this site was unknown. Whether the male that was roosting at the nesting place bred elsewhere in that year was unknown.

As the breeding season progressed remote-roosters were more often unable to return to the principal roost by dark. Then, a secondary roost, closer to or on the nesting place would be chosen, and thereafter frequented. The behaviours which surrounded the choice of secondary roost sites by two breeding males which roosted remotely, were observed on 4 occasions (2 each). In all four, the male had stayed at the breeding area later than usual, and was away from the primary roosting site when it started to rain or darkness fell. When not at their own nesting place, all of the secondary roosts of remote-roosters were in nesting places or near the principal roost sites of other breeding males. When they later abandoned these secondary roosts, they generally moved their roost onto their nesting place. Although I did not observe any moves from principal remote-roost-site to a roost at the nesting place which were more than two staged, they probably occur.

Roosting behaviour was not examined for all the breeding Sparrowhawks in Edinburgh, so I do not know how common remote roosting was, or if it was characteristic of a certain part of the study area.

4.3.1.3.2 Non-breeders

In the spring, non-breeders (4 males,1 female; Appendix 2, Figures 4.10 - 4.14) were less tied to the principal roosting site, particularly as May approached. Twenty-eight percent (N=196) of roosting events for these birds were away from the primary roost, over twice the rate found in home-roosting breeders, a deference significant at the 0.5 level (χ^2=5.1, df=1, P<0.05). Fifty-three percent of the secondary roosting events occurred in the 10 days prior to mean egg-date for that year.

Non-breeders used sites, both as principal and secondary roosts, which were located on the nesting places of other Sparrowhawks (41 nights, 5 individuals). For 3 male and 1 female non-breeder, the occupancy of a secondary roosting site which was also the nesting place for other Sparrowhawks was observed 14 times. In other cases, the secondary roost site was not on an occupied nesting place. After roosting on a secondary roosting site, another move was made by the non-breeder in 1 or 2 days in 73% of the instances. In 8 of 18 cases, the abandonment of a secondary roost site by a non-breeder was known to be preceded by an aggressive interaction with at least one member of a resident pair (Chapter 6). The circumstances surrounding the movement in the other 10 cases were unknown. In 2 of the 3 cases in which a secondary roost was used for more than 2 days, the roost was at an active nesting place, but the resident Sparrowhawks did not roost there at the same time.

In some cases secondary roosts of non-breeders were not located on the nesting places of other Sparrowhawks. At these places no aggression was observed that might have caused movement to another roost site. As elsewhere, movement from these roost sites which were not also occupied nesting places could have been influenced by weather or dark-fall.

Wet weather and dark-fall did not seem to be always related to roosting behaviour in non-breeders. In 24% (N = 55) of the observed secondary roosting events by non-breeders, roosting occurred before dark-fall, during dry weather. This did not differ significantly from the breeders in which roosting at a secondary site prior to darkfall was only witnessed once (N=10). Some of these occurred in late spring, on active breeding places of other Sparrowhawks where the non-breeder had been an 'intruder' during the day (Chapter 6).

When non-breeding Sparrowhawks moved from secondary roosts they usually returned to their principal roost (18 of 25). Even if a non-breeder roosted principally at the nesting place of another Sparrowhawk, it would return there after being chased from a secondary roost site.

Table 4.2 summarizes the roosting behaviour of Sparrowhawks in Edinburgh.

Table 4.2 Roosting behaviour of radio-tagged Sparrowhawks in the spring in Edinburgh, 1986-1989.

	Number of nights (%) at roost	
	Primary	**Secondary**
Breeders		
Remote males	42 (84)	8 (16)
Remote females	12 (86)	2 (14)
Non-breeders		
Males and females	141 (72)	55 (28)

4.3.1.3.3 Replacements

In one case, a colour-marked, yearling female roosted on a nesting place occupied by another female. Two days later the initial resident female was replaced by the yearling. During those days, aggressive chases by both intruder and resident were observed (Chapter 6). The fate of the replaced female was not known. She was not seen again. Details of the roosting behaviour of the intruding female were not completely known since her radio-tag was lost before she replaced the original female. She had been roosting principally at a site 1.8 km away earlier in the spring. Chapter 6 gives details of her behaviours during this time.

Also, an initially unpaired yearling male (Appendix 2, Figure 4.4) replaced an established adult breeder (Appendix 2, Figure 4.3) late in the spring. The yearling was tagged 5 days prior to the death of the adult. It was trapped on a neighbouring nesting place occupied by another adult male. On 3 of the days in which both yearling and adult were being monitored, they roosted in the same area, a wood 1.7 km from the eventual nesting place. On the other days the adult roosted either at the nesting place or at a place part-way between the nesting place and his principal roost. After the death of the adult, the yearling continued to use the remote roost as its principal roost for at least 5 days, even though it associated itself with the nesting place of the adult it replaced. After this time, and at least 15 days before the first egg was laid, the replacement male moved his principal roost to the nesting place.

4.3.2 Ranging behaviour

More males were radio-tagged than females. Appendix 2 represents the maximum polygon area (mpa) for the birds monitored in Edinburgh. Too few female ranges

were known to examine the variation in range sizes in different seasons, for different age-classes, and between breeding and non-breeding females.

In Edinburgh, the size of male Sparrowhawk ranges varied with age and whether or not the individuals bred after being radio-tracked. There was no significant difference in the seasonal range size of males. There was a significant difference between the mean range sizes of all the males and all the females (Unpaired t-test (2-tailed) df=17). See Tables 4.3 and 4.4.

Table 4.3 Mean range size (hectares) of Sparrowhawks in Edinburgh, 1987 and 1988. (Y=yearling, A=adult)

	Sex	N	Age	Mean Area ± S.E
Winter (Oct.-Dec.)				
Non-breeders	Male	2	2Y	529 ± 76.5
	Female	1	1Y	614.4
Breeders	Male	2	1Y,1A	440 ± 40.0
	Female	2	1Y,1A	687 ± 68
Spring (Jan.-May)				
Non-breeders	Male	4	4Y	642 ± 17.2
	Female	1	1Y	989
Breeders	Male	6	1Y,5A	403 ± 21.5
	Female	1	1A	683.5

Among non-breeding male Sparrowhawks no significant difference was found between the spring and winter range sizes (Unpaired t-test (2-tailed) df=4) However, non-breeding males did have significantly larger ranges than breeding males (Unpaired t-test (2-tailed)), both overall (df=12) and in the spring (df=8), though not in the winter (df=2)(Table 4.4).

Table 4.4 Comparisons between range sizes of Sparrowhawks in Edinburgh, 1987 and 1988. (Unpaired t-test, df = N-2; NS=not significant)

Comparison (N)	Probability (2-tailed)
All males vs all females (19)	0.002
Male breeders vs male non-breeders (14)	0.0001
Male breeders in spring vs male non-breeders in spring (10)	0.0001
Male breeders in winter vs male non-breeders in winter (4)	NS
Male non-breeders in winter vs male non-breeders in the spring (6)	NS

There was some overlap in the ranges of adult breeding males which occupied neighbouring territories. The amount of overlap varied between neighbouring males, and was probably linked to male and habitat quality, since this affected the size of Sparrowhawk ranges (Newton 1986). Appendix 2, Figure 4.22 overlays the range maps of adult males breeding on neighbouring territories in Edinburgh.

For 3 breeding males, roosting behaviour in the early spring increased the range (Appendix 2, Figures 4.3-4.5). The mean area with the roost of 424.5 $\pm$ 31.8 hectares was not significantly different (Paired, one-tailed t-test; df=4, t=2.87, P=0.051) from the 316.0 $\pm$ 12.5 hectare mean without the roost.

I examined the number of roost sites used in the spring-time (during the 10 days prior to egg laying in breeders, and during the 10 days prior to mean egg date for non-breeders) by male Sparrowhawks. Range size was positively correlated to the number of roost sites (Spearman Rank Correlation (two-tailed), N = 11; P < 0.02) at that time of year.

The range of the one radio-tagged bird which replaced an established breeder was unusual in that it extended only to the east of the roosting site (Appendix 2 Figure 4.4 (a)). Usually, principal roosts of unestablished birds were somewhere in the middle of the range. This assessment however, may be biased because the focus was on observing the breeding behaviours of established breeders at the nesting place, and 5 days is a relatively short time to determine the range of a Sparrowhawk. Still, 24 radio-locations (which were independent of behavioural observations at the

nesting place) taken at different times of the day were mapped; they were all east of the roosting site.

After the death of the original breeder, the range of the replacement was reduced in size, although he still roosted remotely. The amount of time he spent at the nesting place during the day increased. (Chapter 6). His range was further reduced when he moved his principal roost to the nesting place (Section 4.3.1.3.3). See Appendix 2 Figure 4.4 (a-c).

4.4 Discussion

In general, the roosting behaviour of the Edinburgh Sparrowhawks was similar to that of Sparrowhawks in the rural areas in most respects (Marquiss and Newton 1981; Newton 1986). In the spring, non-breeders used significantly more roost sites than breeders, both in the city and elsewhere, and although yearlings used more roost sites than adults in the winter in both areas, the relationship was not significant in the city .

There were some differences in the roosting behaviours of the urban Sparrowhawks and those observed in the rural areas. In Edinburgh in the winter the number of roosting sites used by adult (but not yearling) Sparrowhawks was significantly higher than the number of roosts used by rural Sparrowhawks ($t=4.34$, $df=14$, $P<0.01$). Breeding birds in the rural areas were found by Newton (1986) to roost virtually exclusively on the nesting place. Although true for some breeders in Edinburgh, there were exceptions. Also, the existence of some established breeders which roosted in places remote from their nesting place was different. These differences in roosting behaviour between rural and urban Sparrowhawk populations could have resulted from greater human disturbance at some roosting places in the city, although variations in the quality of habitats may also have influenced roosting behaviour.

Birds were not radio-tracked throughout the year so the establishment of principal roosting sites could not be investigated thoroughly. However, for birds which were successful breeders at a particular nesting place in any one year, it was probably advantageous to roost on the same site during the following winter. By doing so, the surrounding territory would be known, and presumably could be hunted and defended more efficiently. In as much as winter roosts represented a centre of the winter

range, and often birds which used a particular nesting place in one spring roosted there in the following winter, winter ranges of urban Sparrowhawks were closely associated with their previous nesting place. This association between nesting place and winter roost has been found in rural nesting Sparrowhawks (Marquiss and Newton 1982), and urban nesting Merlins in Saskatoon, Canada (Warkentin and Oliphant 1990). Having survived the winter, Sparrowhawks (and Merlins) that had roosted over-winter on a site should then be at an advantage in setting up a nesting place there in the spring.

Within Edinburgh, birds which did not breed in the spring-time either before or after radio-tracking, were less tied to a single roost than birds which did. Similarly, in southern Scotland, yearlings (mostly non-breeders) showed less fidelity to one roost site, and spent more of their time away from nesting areas (Marquiss and Newton 1982). Similar roosting/ranging behaviour has been reported for a non-breeding, urban Goshawk in Germany during the winter (Deitrich and Ellenburg 1981).

In Edinburgh roost sites are probably not limiting, given the number and variety of trees and bushes in the city, and the variety of places in which Sparrowhawks were known to have roosted. In Saskatoon, Canada, Warkentin and James (1990) propose the availability of suitable winter roosting sites as a possible limiting factor in colonization of the northern Great Plains by Merlin.

Despite the many potential roost sites, some birds regularly roosted close to one another. Aggression was witnessed, but not in all cases. If there was competition for roosting sites I could not quantify it. In many instances, particularly as egg date approached, aggressive behaviour displayed against other Sparrowhawks could have been associated with defense of the nesting place and/or the mate (Chapter 6), and not related to roost defense *per se*. I could not determine whether aggressive displays were more intense during the spring than during the winter, but they were witnessed more often as egg laying approached (Chapter 6). Roost defence by adult Sparrowhawks in rural areas has been observed (Marquiss and Newton 1982).

Roost sites were not chosen at random since leaved trees were always used. For urban Merlin, Warkentin and James (1990) were able to distinguish roost trees from random trees by a set of characteristics which probably enhanced protection from potential predators. Some particular fidelity must have been associated with

Sparrowhawk principal roost sites since they were returned to after nights spent in other places. Early in the breeding season this fidelity was strong enough to cause some breeding individuals to roost principally away from the nesting place. The choice of a secondary roost site probably had to do with convenience and security. Secondary roosting sites were often chosen during bad weather or impending darkness. Some individuals returned to secondary roost for a number of consecutive days, but this could be altered by an aggressive resident Sparrowhawk. The presence of either Tawny Owls or Kestrels did not seem to affect the choice of roost area (either principal or secondary), although it may have affected the choice of roost tree. The area where a Sparrowhawk would roost was probably influenced by whether their presence was noticed by other (particularly breeding) Sparrowhawks using that area.

The fragmented nature, and high level of human disturbance at some places in the city might have made them unsuitable as roosting sites for Sparrowhawks. Different areas within the city are subjected to different levels of human activity at different times of the day. Places in which Sparrowhawks might be able to nest, and be active in the day-time, may not have felt secure enough for a roosting individual at night because of disturbances such as street lights and traffic. Some places which were quiet at night and suitable as a roost site, were subject to high levels of day-time, human activity which made nesting there impractical. The factors important to roosting site choice could not be determined in this study.

The roosting behaviour displayed by Sparrowhawks seems influenced by the time of the year, and during spring was probably connected with the approach of the egg-date, the reproductive state of the individual, and the weather. For individuals which were able to breed, a site would need to provide both security and have the qualities of a good nesting place. The most efficient way a breeding individual had of defending a good quality nesting place would be to roost on it. As the egg-date approached, both breeders which were nest-roosters and remote-roosters spent more nights at the nesting place. This was likewise associated with an increase in day-time attendance at the nesting place (Chapter 6).

For a non-breeder, roosting sites needed to provide security from other Sparrowhawks, and other predators. Since these birds could commute to favourable hunting areas, so the roosting places did not necessarily need to be of high quality in terms of nesting. As spring progressed, non-breeders used more roosts. Marquiss

and Newton (1982) suggested the number of roost sites could be linked to non-breeders being unable to hunt effectively, and spending more time, particularly late in the day, foraging a long way from the main roost. The number of roost sites used by individuals could also be associated with an increase in breeding-place prospecting behaviour by non-breeders, and/or an increase in the defensive behaviour displayed by territory holders. The case of a yearling male which roosted at a site which was located on the edge of its range even before it managed to occupy a nesting place (Appendix 2, Fig 4.4), suggests that it was prospecting for a breeding place, and that this affected its ranging behaviour. Chapter 6 illustrates both an increase in territorial defense and an increase in territorial intrusions by non-paired individuals, both male and female, as the egg-date approached.

For individual Sparrowhawks, particularly yearlings, which at the beginning of the winter were unlikely to breed in the coming spring, the move onto a nesting place might occur rather late in the season as the result of the death of a breeder on a good quality territory, or by settling for one of lower quality. Secondary roosting places were chosen by birds in all reproductive categories as a result of weather or dark-fall catching individuals away from the principal roost For potential breeders that were not paired, secondary roosts sites may have been a result and means of prospecting for a place in the breeding population

In the winter, Sparrowhawk range size was not significantly correlated to the number of roost sites. The winter ranges of too few adults were known. Yearlings (whose winter ranges were significantly larger than those of adults in rural areas) did not have significantly more roosting sites than adults. In the spring (among home-roosting breeders) however, range size and roost numbers were correlated since (at least in males) breeders were usually adults, had fewer roosts, and had smaller ranges than non-breeders --- a finding consistent with that of Marquiss and Newton (1982). In the cases of males, the existence of remote-roosting, breeding Sparrowhawks, with principal roosting sites on the edge of their ranges suggests that, at certain times of the year, the location of roost sites can expand a bird's range. Not enough information was collected for females to make comparisons.

Ranges of Edinburgh Sparrowhawks showed many of the same characteristics found in rural, southern Scottish Sparrowhawks (Marquiss and Newton 1982, Newton 1986), and Goshawks (Kenward 1977, and Kenward *et al.* 1981). Winter ranges were usually larger than those in the spring, females usually had larger ranges than

males, yearlings larger ones than adults, and non-breeders larger ones than breeding Sparrowhawks. Also, Sparrowhawk ranges (at least in males in the spring) were correlated with the number of roost sites.

More aggressive interactions were observed during the spring (Chapter 6) than the winter, but whether in defense of a food resource, nesting place or mate, I could not determine. In Edinburgh, the relatively few radio-tracked individuals, and the fact that a large proportion of the breeding male population was adult, confused the relationship between range size and reproductive success. Marquiss and Newton (1982) were able to correlate range size and breeding success (inversely) for rural Sparrowhawks.

A relationship between range size/ranging behaviour and prey densities has been shown in rural Sparrowhawks (Marquiss and Newton 1982, and Newton 1986), Goshawks (Kenward 1982; Kenward and Widén 1989; Deitrich and Ellenburg 1981), Kestrels (Village 1990), and other raptors (See: Newton 1979). In the part of Edinburgh where radio-tagged birds ranged, prey was plentiful (Chapter 2), but the hunting efficiency of the Sparrowhawks, and therefore the range size, may have been affected by other factors, such as human disturbance, the sizes of woodland stands, age, and experience of the Sparrowhawks. Despite the amount of prey, the size of the ranges of radio-tagged Sparrowhawks in Edinburgh were similar to the size of Sparrowhawk ranges in relatively poor habitat in southern Scotland (Marquiss and Newton 1982), but in the city the habitat in which the Sparrowhawks could hunt efficiently was more fragmented.

In rural areas, differences in hunting habitat preferences between males and females in a pair also contributed to their ranges being different (Newton 1986). This was probably less true for the Edinburgh Sparrowhawks since extensive woodlands (favoured by rural males) are rare in the city.

In Edinburgh, the fact that non-breeding Sparrowhawks have a larger mean range size than breeders is confused since most non-breeders were yearlings and most breeders were adults. I suspect that the range of a Sparrowhawk in the spring, which has failed to attract a mate and establish a territory, may be to some extent result from increased prospecting in the late spring in search of a breeding opportunity. Chapter 6 discusses the increase in intrusions by non-pair (and in some cases non-breeding) individuals.

Ranges of Sparrowhawks within the city in both winter and early spring overlapped to a large extent. This is similar to Sparrowhawks in rural areas (Marquiss and Newton 1982). In the spring and early summer less overlap was obvious probably because of increased defensiveness of territory holders, increased attendance at the nesting place by the breeders, and an increase in the prey density as the chicks of prey species fledged.

CHAPTER 5

Breeding Performance

5.1 Introduction

Data on the breeding performance of raptor species are usually relatively easy to collect because during the breeding season birds are tied to a nesting place, where eggs and young can be counted. Nesting habitat preferences and the number of eggs and young are the only information available for certain raptor species. For a review of the techniques for the assessment of habitat, and the reproductive success of raptors see: Newton 1979, Mosher *et al.* 1987, and Steenhof 1987.

In British Sparrowhawks, the variation in breeding performance in different areas, in different years, and in pairs with different reproductive experience has been investigated in detail (Moss 1976, 1979; Newton and Marquiss 1976, 1981,1982, 1984; Newton *et al.* 1979, 1981, 1983; Newton 1976a, 1985; Petty 1979), as have the effects of organochlorine pesticides (Newton *et al.* 1979). Sparrowhawk nesting habitat has been studied by Hald-Mortensen (1974) in Denmark and by Newton (1986) in Britain.

This chapter investigates the reproductive performance of the Edinburgh Sparrowhawks. Performance is viewed in relation to the available nesting places and their structure, the age and experience of the breeders, and weather conditions, as well as the influence of the urban environment.

5.2 Methods

5.2.1 Availability and occupancy of nesting places

I began by identifying all areas where it seemed possible for Sparrowhawks to breed within the city. Definitions of 'occupied' and 'potential' nesting places are given in Chapter 1. Both male and female Sparrowhawks (both singly, and with a potential mate) were known to frequent some nesting places before nest-building, but move to other nesting places to breed (Chapter 6). Therefore, nesting places were only

considered to be 'occupied' when nest building was evident (Chapter 1).

5.2.2 Nesting place description

Appendix 1, Table 5.1 lists the full range of variables examined to describe the nesting places of Edinburgh's Sparrowhawks. These were similar with those used in a recent study of an urban population of Merlins *(Falco columbarius richardsonii)* in Saskatoon, Canada (Warkentin and James 1988). Most of these variables are self-explanatory. The complexity of the woodland in which Sparrowhawks nested was measured by the combined variables: species composition of nest wood site, numbers of conifers greater than 5m in height, numbers of conifers less than 5m in height, numbers of broad-leaved trees greater than 5 m in height, and the number of those less than 5m in height, along with the assessment of shrub cover in an area within 10 m of the nesting tree. Human influences on the nest site were assessed through the variables: 'disturbance' and the distance to regular human disturbance. 'Disturbance' was based subjectively on the number of people frequenting the nesting place , and classed as high, medium, and low. An area of 'high' disturbance would be a place where on most days a large number of people (> 50) pass within 10 m of the nest or the exposure of the nest is such that people can see into it, an example being a busy city park. 'Medium' disturbance describes places where on most days a moderate number (10-50) of people pass within 10 m of the nest tree, such as in an old cemetery, or on waste ground where people might walk their dogs. An area of 'low' disturbance is a place where visits by humans are infrequent (<10/day), such as the grounds of some hospitals, in larger woods, or disused railway land. Mean values are given with the standard error, unless otherwise stated.

5.2.3 Breeding performance

Data on breeding performance were gathered from periodic nest checks. Where possible the age and identity of the breeders was determined (See Chapter 1), and related to breeding performance.

5.2.4 DNA fingerprinting

Blood samples were taken from as many of the full-grown Sparrowhawks and chicks as possible (See Chapter 1). These samples were used to test paternity by DNA-fingerprinting techniques. Techniques for DNA fingerprinting Sparrowhawks, using two different probes (Probes 33.6 and 33.15), were developed in the laboratory of

Dr. D. Parkin of the Department of Genetics, University of Nottingham. Roy Carter, working with Dr. Parkin, developed the probes, conducted the tests, and confirmed the results. Specific details of DNA fingerprinting laboratory protocol, including preparation of reagents are set forward in Carter 1991.

Generally, fingerprinting was done in nine steps: 1. Collection of blood, 2. DNA extraction, 3. DNA restriction, 4. Electrophoresis, 5. Blotting, 6 Prehybridization, hybridization and washing, 7. Preparation of hybridization probe, 8. Autoradiography, and 9. Scoring of gels.

5.2.4.1 Blood collection

Blood was collected from all birds caught and rung during the study. A particular effort was made to sample the blood of complete families and suspected cuckolds. More effort was put into the capture and blood sampling of individuals for whom behavioural data was being collected.

Blood was collected from the brachial vein. The vein was pierced using a sterile needle at the point where it is close to the surface near the elbow. Usually, 2-5 drops of blood could be collected before bleeding stopped. This was enough for the fingerprinting process.

Blood was stored in 1 ml vials, and frozen (-10 ^{o} C) until the end of the season. All samples were then sent by mail for analysis.

5.2.4.2 DNA extraction

Fifteen microlitres of whole blood was suspended in 600 µl of isotonic buffer. The cells were lysed by the addition of sodium dodecyl sulphate solution. Lysis causes the release of nucleases. These are inactivated by incubating with 15 µl of proteinase K solution overnight at 55 ^{o}C.

Protiens contaminating the DNA are denatured and removed during a series of extractions with immiscible organic solvents.

To the DNA solution is added 500 microlitres of buffered phenol, the phases are mixed for 15-30 minutes then separated by centrifugation. Protiens partition to

the lower organic phase or precipitate at the solvent interface. The aqueous phase is recovered and additionally extracted either with repeated phenol or phenol/chloroform/isoamyl alcohol until no further precipitation occurs at the interface. The final traces of phenol are removed by a brief chloroform/isoamyl alcohol extraction. The DNA is then recovered by the addition of cold (-20 ^{o} C) absolute ethanol for 30 minutes at -20 ^{o} C which causes the precipitation of the DNA. This is collected by centrifugation. Traces of ethanol are removed by drying *in vacuo* and the DNA is dissolved in TE buffer at 55 ^{o} C overnight.

5.2.4.3 DNA restriction

The genomic DNA isolated is a suitable substrate for digestion with a variety of restriction enzymes. Ideally a restriction enzyme is chosen which cuts frequently in most genomic DNA but not within tandemly repeated minisatellite sequences, a variety of such 'four base pair' restriction enzymes exist, e.g. Hae III, Alu I, and Hinf I, although their suitability varies with different species.

An aliquot containing an excess of genomic DNA is digested to completion with the chosen 'four base pair' restriction enzyme according to the manufacturers instructions, usually overnight and in the presence of Spermidine HCl.

The extent of the digestion is monitored by the 'minigel assay', a small aliquot is electrophoresed through an agarose minigel, stained with ethidium bromide and the resulting smear is examined. All samples are quantitatively assayed flourometrically, and are adjusted to 0.15 $\mu g\ \mu l^{-1}$.

5.2.4.4 Electophoresis

DNA fragments are separated by electrophoresis according to size by molecular sieving through an agarose gel under the influence of an applied electrical field.

An agarose solution is prepared, cooled to 55 ^{o}C, and poured into a gel-mould to set. The gel is placed into an electrophoresis tank containing 2.5 l of 1 X TAE electophoresis buffer. The samples and appropriate molecular weight markers are heated to 65 ^{o}C for ten minutes, then rapidly quenched in ice. They are micropipetted into the preformed sample wells of the gel. The samples are allowed to equilibrate with the electrophoresis buffer for ten minutes prior to commencing

electrophoresis. Electrophoresis is long and slow (40-72 hours at 40V) in order to minimize 'band smiling'.

5.2.4.5 Blotting

For ease of handling the DNA fragments are transferred (Southern transfer) from the gel to a solid support matrix (nitrocellulose) by capillary blotting, thus maintaining their relative positions. After transfer the DNA is fixed to the membrane by drying *in vacuo* for 2 hours at 80 ^{o}C

5.2.4.6 Prehybridization, hybrdization, and washing

The probe is prepared and is used to wash the filter, in order that it might bind to homologous sequences immobilized on the membrane surface.

Non-specific hybridization of the labeled probe to positively charged sites on the membrane surface is prevented by a prehybridization stem. The membrane is washed with proteinaceous 'blocking' agents at the desired strigency for several hours. This can be done in either bottles or cake boxes depending upon the number of filters to be done.

Stringency, which regulates the match between probe and target is varied during hybridization. For Sparrowhawks a moderate stringency (1 X SSC at 65 ^{o}C) was employed.

Non-bound probe is removed from the membrane by washing at 65 ^{o}C in several changes of wash solution (1 X SSC, 0.1% SDS).

5.2.4.7 Preparation of a hybridization probe

A hybridization probe is a piece of nucleic acid which can be hybridized to specific target sequences, and which is 'labeled', allowing their detection. The probes used for Sparrowhawks were RNA probes and were radioactively labeled.

The minisatellite region from the multilocus fingerprint probes 33.6 and 33.15 were subcloned into a transcription vector.

Radiolabeled (^{32}P) RNA was prepared by transcribing from T_7 RNA polymerase promoter, multiple RNA copies of the minisatellite and incorporating into them alpha- ^{32}P CTP using a commercial kit .

5.2.4.8 Autoradiography

Labeled probes hybridized to target sequences on the membrane may be detected by autoradiography. ß radiation emitted from ^{32}P labeled nucleotides incorporated in the probe will expose X-ray film. Intensifying screens are used for initial exposures to amplify the image. Exposures without amplification offer improved resolution, but require much longer exposures.

After washing is complete the filters (while still damp) are wrapped in clear kitchen wrap and exposed to pre-flashed X-ray film for 4 hours at -80 ^{o}C in a cassette with two tungsten intensifying screens. This autoradiograph is developed photographically and used to gauge additional exposures with screens, if necessary, or exposures without screens.

5.2.4.9 Scoring of gels

The presence or absence of particular bands of DNA is checked relative to the other members of the family. The presence of particular bands of DNA in a young Sparrowhawk is determined by those bands also being present in either the mother, the father or both parents. If bands appear in the offspring that are not also represented in the parents, it is likely that the chick is a product of a mating not between the individuals acting as parents. In the case of the paternity checks carried out on the Sparrowhawks, if one probe brought the parentage under suspicion, this result was confirmed by the use of the other probe. The data was also analysed by a more stringent statistical means which compares the band sharing between each individual, and both of its putative parents, and then assigns a probability for each band occurring by chance. Scoring was made easier by arranging the fingerprints of the offspring between those of the putative parents.

Free-flying males were more difficult to catch, limiting the ability to test whole families. Behavioural information suggested certain males to be possible cuckolds (Chapter 6). Where possible, the possible paternity of any mismatched offspring was tested using two different probes. Neighbouring male Sparrowhawks were tested

as possible cuckolds of each other where possible. Fingerprinting results presented here are preliminary; more complete results shall be presented in the future. Plates 5.1 and 5.2 show the DNA fingerprints of two families of Sparrowhawks in Edinburgh in which some of the offspring were not the product of the putative father.

5.2.5 Weather

Weather data were from the meteorological station at the Royal Botanic Gardens, in the middle of the study area. Data on average monthly temperature, number of days in which the air temperature dropped below freezing (freeze-days), monthly rainfall, number of days in which the rainfall exceeded 0.2 mm (rain-days), and the number of snow-days (lying at 0900 hours) were examined -- Appendix 1, Table 5.2

5.2.6 Human influence and pollution

Human influences varied and were sometimes hard to quantify. Some human influences on prey levels in the city are discussed in Chapter 2. Here, the effect that people had on production by causing nest destruction, and the levels of pesticides in unhatched eggs is examined. Mortality and predation of Sparrowhawks, and the levels of pesticides and other pollutants in their corpses are dealt with mainly in Chapter 3, and are discussed here only in reference to possible effects on productivity. Toxic residue analysis carried out by the Monks Wood Experimental Station of the Institute for Terrestrial Ecology determined the amount of DDE (a metabolite of the insecticide DDT); HEOD (active ingredient in dieldrin; a metabolite of aldrin); HCB (primarily an industrial by-product which is moderately toxic to birds); HCH (from Lindane); HE (from heptachlor); PCB's (polychlorinated biphenyls, industrial toxin); and the heavy metal, Mercury. Methodology for contaminant analysis is set forth in Cooke, *et al.* (1982).

5.3 Results

5.3.1 Availability and occupancy of nesting places

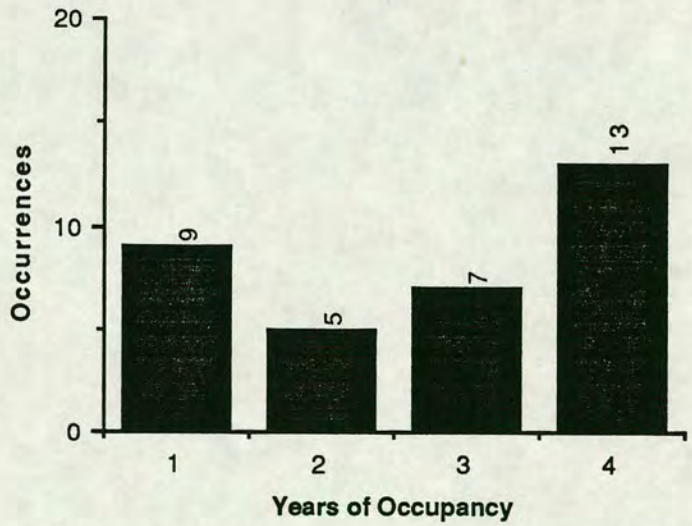
Seventy-four woodlands 'suitable' (in terms of the presence of likely nesting trees and distance from other known Sparrowhawk nesting places) for Sparrowhawk nesting were identified within the city (Chapter 3); 51 (69%) of these (Appendix

2, Figure 3.1) showed signs of attempted breeding by the presence of a nest structure; 39 (77%) of the sites were occupied at least once during the study. In the other 12, recently built nests indicated that the place had been occupied in the recent past. In any one year, approximately 34% of the potential and 50% of the known nesting places were occupied.

There was no significant variation in the number of occupied sites in different years of the study (Table 5.1), but not all sites were occupied equally often. Thirteen sites were known to be occupied in all 4 years of the study, 7 in 3 years, 5 in 2 years, and 9 in one year (Figure 5.1). This was significantly different from random (χ^2 = 50.9; df=3,P < 0.01). At 5 sites I was unsure of the occupancy in all four years.

If all sites that were identified as having produced at least a nest in the recent past had been occupied in all 4 years, there would have been a total of 204 nesting attempts. In total 102 nesting attempts were recorded. This does not mean that only 50% of nesting opportunities were taken, for some places might have been alternates for others, but this could not be confirmed over this relatively short study.

Figure 5.1 Occupancy of Sparrowhawk nesting places in Edinburgh, 1986-1989.



If a less rigid definition of occupancy is applied, and all places where a male and female were seen together in the early spring are included, then at least 87% of the potential nesting places would have been occupied at some time during the study.

5.3.2 Nest place description

5.3.2.1 Nest woodland area

There was some variability in the area of woodland in which Sparrowhawks nested. One wood was over 80 hectares, while the spacing between trees in some other nesting places made it difficult to describe them as 'woods'. In at least 3 nesting places, nests were placed in trees separated from each other or another stand of trees by more than 20 m.

Although most woodlands within the city were only large enough for one nesting place, three woods had two, and one (Corstorphine Hill), had at least 3 places available in any one year. Almost half of the nesting places were in woods between 2 and 6 hectares in area.

5.3.2.2 Nest woodland structure and nest tree description

Nesting woods varied greatly in structure, including isolated trees in fields and parks, patches of willow (*Salix* sp.) and alder (*Alnus* sp.), plantation-type conifer stands, and mature, mixed woods.

A wide variety of tree species was selected for nesting, partly because many gardens contained exotic species. Sparrowhawks nested in both conifers and broad-leaved trees, but conifers were used more often, for 78 of the 97 (80.4%) nests found. The most common nest tree was the Scot's Pine (*Pinus sylvestris*, (37 out of 97, 38%)), followed by European Larch (*Larix decidua*), and Cedars (*Cedrus* and *Thuja* sp.). Sycamore (*Acer pseudoplatanus*) was the most commonly used broad-leaf tree. The density of the woods in which nesting occurred varied; only very dense, relatively young (<20 years old) stands were not used for nesting.

In size, nest trees varied from over 30 metres high (Sycamore) with a circumference at breast height (cbh) of more than 3m (large Chestnut (*Aesculus* sp.)) to a dead Sitka Spruce (*Picea sitchensis*) 2.1 m in height, with a cbh of 0.31m. The average height of nesting trees was 15.07 $\pm$ 0.49 m, and the mean circumference was 1.32 m. No significant difference was found between the size of coniferous and broad-leaved nest-trees, which averaged 15.69 m and 14.85 m in height and 1.26 m and 1.54 m in circumference respectively.

Mostly nests were built on bare branches that afforded a level substrate, but some were built on top of existing nest structures (previous Sparrowhawk nests, squirrel dreys, Corvid and pigeon nests). Mean nest height was 10.63 ± 0.45 m (Conifers: 10.97 m, broad-leaves: 9.78 m). For all sites, the nest height was over two-thirds (mean = 0.77) of the tree height, which was consistent with Newton's (1986) findings elsewhere.

Nesting places varied widely, from mature mixed forest with a relatively dense understory of shrubs, to young and closely spaced conifers with no shrub layer, or widely spaced trees in a garden situation having no undercover. The 'typical' nesting place had (within 10 m of the nest tree) 2-3 individual conifers or 2-3 deciduous trees of a height greater than 5 m, virtually no conifers and 3 deciduous trees of less than 5 m. The shrub cover was usually less than 5%.

The mean distance to regular human disturbance was 24.1 ± 3.78 m (N=96). In many cases the distance to the wood edge and the distance to human disturbance were the same. Thirty-one nests were in areas of low human disturbance, 45 experienced medium, and 20 high levels of disturbance. Six nesting places experienced a drastic change in the level of human disturbance during the breeding season. Since nests destroyed early in the breeding season were usually replaced, there was no difference between the number of pairs that failed (or in the overall production of chicks) in these different categories. Those in heavily used areas were more likely to be destroyed due to direct human interference (4 cases, 20%) while those it the areas of low and medium activity suffered little from obvious human intervention (two cases were documented, 2.8%). Nests less exposed to human disturbance failed for other reasons (i.e. predation and bad weather; Section 5.3.4). All of the nests which experienced a dramatic change in the level of human disturbance failed to breed successfully, even when the change was from a high level of disturbance to a low level. No obvious physical differences between places occupied during the study and those occupied prior to the study were noted.

5.3.3 Performance

Table 5.1 shows the reproductive performance of the Edinburgh Sparrowhawk population. These data fall into the range of Sparrowhawk production statistics found in studies elsewhere (Newton 1986). See Chapter 1 for details of terminology, and

methods used in evaluating production.

5.3.3.1 Nest and egg production

Nests were started mostly in April, but some as early as November. Although nests were easily identifiable at an early stage of construction, it is likely that I missed some nests which were not completed. Still, in 93% of the nests that were located in the early breeding season, at least one egg was laid.

Table 5.1 Sparrowhawk production in Edinburgh 1986-1989 (NA= not applicable. M = male, F = female).

	1986	1987	1988	1989	TOTAL	MEAN	S.E.
NESTS	22	26	27	27	102	25.5	1.19
PROD. NESTS	22	23	25	25	95	23.75	0.75
EGGS LAID	88	95	114	105	402	100.5	5.69
MALE CHICKS HATCHED	30	33	31	38	132	33	1.78
FEMALE CHICKS HATCHED	14	28	49	32	123	30.75	7.21
TOTAL CHICKS HATCHED	44	61	80	70	255	63.75	7.64
MALES FLEDGED	27	31	28	38	124	31	2.48
FEMALES FLEDGED	14	27	44	32	117	29.25	6.21
TOTAL FLEDGED	41	58	72	70	241	60.25	7.12
EGGS/NEST	4.00	3.65	4.22	3.89	NA	3.94	0.119
EGG/PROD NEST	4.00	4.10	4.60	4.20	NA	4.22	0.131
M CHICKS/NEST	1.36	1.27	1.15	1.41	NA	1.29	0.133
F CHICKS/NEST	0.64	1.08	1.81	1.18	NA	1.19	0.123
CHICKS/NEST	2.00	2.35	2.96	2.59	NA	2.47	0.202
CHICKS/PROD NEST	2.00	2.60	3.20	2.80	NA	2.65	0.250
CHICKS/EGG	0.50	0.64	0.70	0.66	NA	0.63	0.044
M FLEDGED/NEST	1.23	1.19	1.04	1.41	NA	1.22	0.13
F FLEDGED/NEST	0.64	1.04	1.63	1.18	NA	1.12	0.13
FLEDGED/NEST	1.86	2.07	2.67	2.59	NA	2.30	0.2
FLEDGED/PROD NEST	1.90	2.60	2.90	2.80	NA	2.52	0.22
FLEDGED/EGG LAID	0.47	0.61	0.63	0.67	NA	0.59	0.04
M FLEDGED/M CHICK	0.90	0.94	0.90	1.00	NA	0.96	NA
F FLEDGED/F CHICK	1.00	0.96	0.90	1.00	NA	0.97	NA
FLEDGED/CHICK	0.93	0.95	0.90	1.00	NA	0.94	NA
% SUCC NESTS	65	68	70	73	NA	69	1.68

The date on which the first egg was laid (egg-date) varied from 28 April to 7 June, but the mean egg-dates varied little from year to year. In 1986 the mean egg-date was 11 May (N=13); in 1987, 14 May (N=18); in 1988, 12 May (N=16); and in 1989, 9 May (N=19). Clutch size could not be examined in relation to egg-date in this study because relatively few clutches were started late in the season. Clutch sizes varied from 1 to 6, but most commonly, completed clutches contained 5 eggs (37%).

5.3.3.2 Chick and fledgling production

A total of 255 young hatched. Once they were half-grown, the sex of the chicks could be determined: 123 were female and 132 male (3 uncertain), a ratio not significantly different from unity (χ^2 = 0.478, df =1). Most commonly, nests contained 4 chicks (32%).

Of the eggs laid, 63.4% hatched. There were many reasons why eggs did not hatch. Some were addled, some had been cracked or pierced while in the nest, some were eaten by predators, and some disappeared from the nests for unknown reasons. The relative importance of the different causes of egg loss could not be assessed. In clutches where none of the eggs hatched, it was usually impossible to discover the cause.

Three clutches (14 eggs) were known to be destroyed by humans. Two of the affected pairs re-laid, both then produced 4 eggs. In some cases it was difficult to determine if the nest had been deserted for other reasons prior to predation, especially when no re-nesting occurred. On one nest a domestic cat was found sitting on 4 fertile eggs. The nest was subsequently deserted, although the female had not been killed. In two cases, predation by Corvids was indicated by the presence of pierced shells. At one, the egg-shells were found at the base of the nest-tree, but I could not determine if they had fallen to the ground before being eaten, or had been predated on the nest. In one case, the wet, windy weather brought down a nest built on a fragile branch. Five eggs were lost, at least 3 of which were fertile.

Some 94.6% of chicks survived to fledging. There was no difference in the survivability of male and female young to fledging age, 94 and 95% respectively. There were equal numbers of broods (10) holding only male nestlings as those with only females; the survival within these broods was similar.

In two cases where chicks were hatched, but not fledged, human interference was the cause. In both, the nest was pulled from its tree. In two instances weather caused the death of nestlings, one due to rain, one due to wind (Section 5.3.4.1). In one nest the adult female was found dead from unknown causes with three dead chicks under her. In all other cases no reason for nestling mortality was found.

Blood samples were taken from 42 full grown (adult and juvenile) birds (both breeding and non-breeding) and 164 nestlings for possible paternity tests. Blood samples were used to test the paternity of 10 complete families (39 chicks). In 8 families, none of the 33 fledglings were genetically mismatched with the putative parents of the pair. Of the other two broods (comprised of 5 and 1 individuals), 1 in each, or 5% of all those tested were not the product of the putative parents (Example in Plate 5.1). In both cases, these chicks could have been related to the breeding female, but were not related to the male, suggesting extra-pair copulations (or sperm storage of a previous mate) rather than 'egg dumping'. During behavioural observations (Chapter 6), the mother of the solitary mismatched chick was seen to engage in extra-pair copulations with an adult male from a neighbouring territory. A fingerprint from this suspected cuckold, indicated that it was not the father of the chick (Plate 5.2).

These results of paternity tests are only preliminary. There was no data on the number or hatchability of eggs produced from either extra-pair copulations or sperm that had been stored within the female reproductive tract.

Plate 5.1 DNA fingerprints of a family of Sparrowhawks in Edinburgh. F is the putative father. B is the putative mother. V, W, X, Y, and Z are chicks raised in that nest. W is related only to the female, not to the male. M indicates an example of a mismatched band

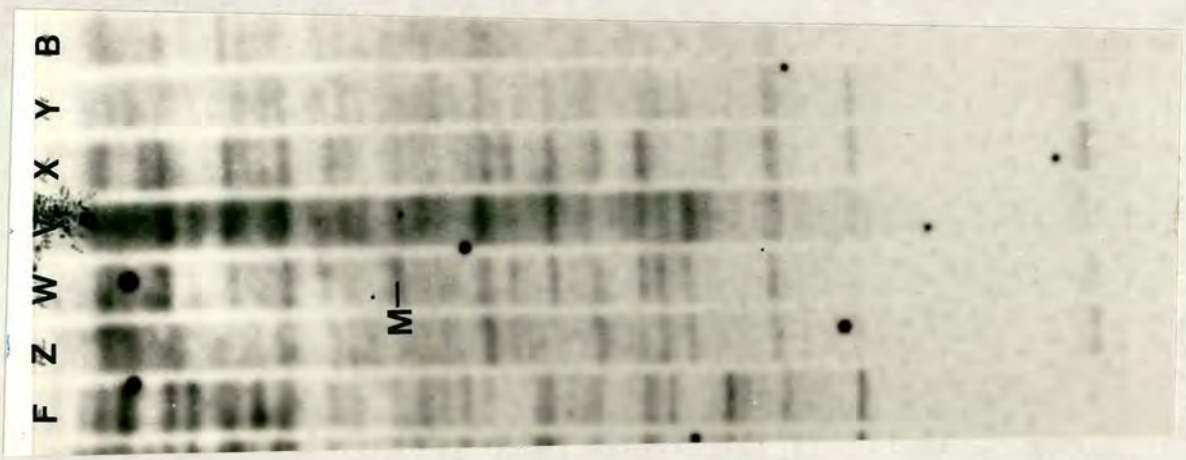
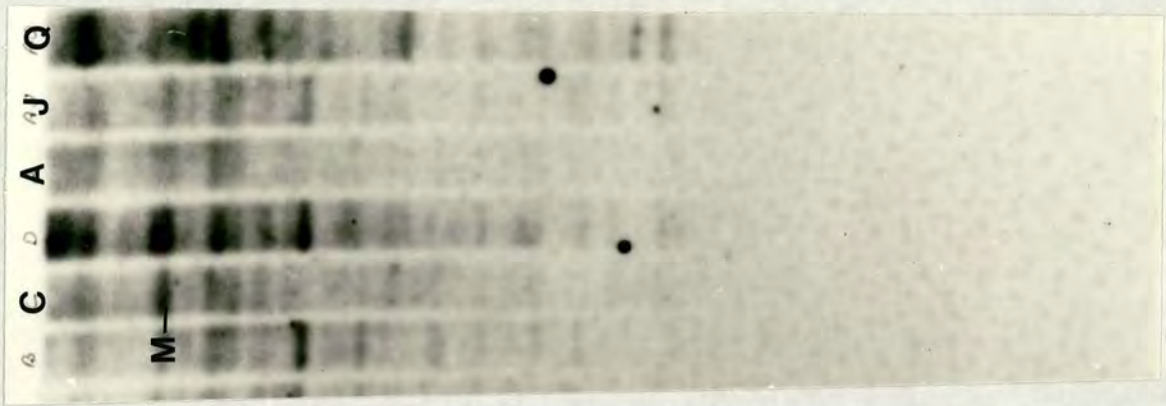


Plate 5.2 DNA fingerprints of a family of Sparrowhawks in Edinburgh, and that of a extra-pair male that was observed copulating with the female. The putative father is Q. The putative mother A. The offspring is C. The suspected cuckold is J. The offspring is not related to either the putative father or the suspected cuckold. M indicates a mismatched band.



5.3.4 Factors affecting production

5.3.4.1 Breeding performance and weather

The weather information was divided to correspond broadly with different phases of the breeding cycle, namely the pre-laying phase, February - April, the egg phase, May - June, and the nestling phase, June - July. With only four years of data, correlations were statistically unprovable. Graphical relationships have been drawn to indicate the weather factors with which breeding performance seemed most highly correlated (Appendix 1, Figure 5.1).

The only weather statistic that had an effect on breeding performance at all stages (whether in terms of nest, egg, chick, or fledgling production) was the average temperature in the pre-nesting part of the year, February-April. The relationships between weather and production variables of urban Sparrowhawks were sometimes similar to the findings of Newton and Marquiss (1986), but they were not as clear cut. Weather during the incubation and nesting stages may have been important because large clutches hatched and survived only in years of warm, dry springs and early summer-like weather. Only in 1988 and 1989, the two warmest, driest summers, did broods of 6 survive to fledging age.

5.3.4.2 Age of breeding Sparrowhawks

5.3.4.2.1 Age of female and breeding success

Yearling and adult females did not differ significantly in production of eggs, chicks or fledglings (Table 5.2), in contrast to findings elsewhere (Newton 1986).

Most commonly, Sparrowhawks of both age groups produced clutches of 5 eggs, accounting for 36.7% of all clutches. Clutches of six eggs were, in all but one case, produced by adult females. Also, nests in which no eggs were produced were exclusively occupied by adult females. For both ages, the most common brood size was 4. For adults, 3 was the most typical number of nestlings, while yearling females most commonly produced 4. The adults produced more of the large broods, and accounted for most of the failures at this stage (Figure 5.2).

Table 5.2 Mean clutch size, brood size at hatching, and number of fledglings (± S.E.) produced in relation to age of female Sparrowhawks (including nest failures) in Edinburgh, 1986-1989.

Age of female	N	No. of Eggs laid	No. of Chicks hatched	No. of Chicks fledged
Yearling	21	4.23±0.23	2.59±0.31	2.44±0.37
Adult	33	4.26±0.21	2.87±0.23	2.76+0.27

5.3.4.2.2 Age of pairs and breeding success

The age of both members of breeding pairs was known in 54 instances. In 33 cases (61.1%) both were in adult plumage. In 17 (31.5%), the male was an adult and the female was a yearling. There was only 1 case (1.8%) of a yearling male paired with an adult female, and only 3 cases (5.5%) where both male and female were yearlings (Table 5.3). This frequency distribution did not differ significantly (Fisher's Exact Test, P = 0.12) from that of a randomly pairing population.

Since such a large percentage of the breeding pairs were adult, the effect of age of the members of the pair on production could not be distinguished from the effect of female age (Table 5.3).

5.3.5 Turnover and production

Another factor which could have affected breeding performance was breeding experience at that nesting place in the previous year. 'Turnover' describes nesting place fidelity, and is defined as the change of a breeder at a particular nesting place from one year to the next (Chapter 1). Turnover can be the product of mortality, non-breeding, or movement to a different nesting place (for methods relating to turnover, see Chapter 3). Details were examined for 1987-1989, separating three categories: (a) pairs in which turnover could be determined for both members, (b) pairs in which it was confirmed for only one member of the pair, and (c) pairs in which it could not be determined for either partner.

Turnover for both members was known for relatively few pairs, but in all years, and in each stage of reproduction (except egg production in 1988), nesting places at which the female remained the same from one year to the next were more productive than at places where the female changed (due either to mortality or movement). This difference was not significant for egg production, but was for both chick and fledgling production (Table 5.4).

Omitting breeding females which were also yearlings (N=12) in order to exclude known first-time breeders, adult females which exhibited nesting place fidelity had, on average, the same number of eggs per clutch (N=15), but both the number of chicks hatched (N=15) and the number of fledglings (N=16) produced were higher than adult females which were new to a site (n=12)(Figure 5.3). Adult females new to a site produced a mean of 2.92 $\pm$ 0.23 chicks and 2.33 $\pm$ 0.27 fledglings while adult females experienced with breeding on a particular site produced and average of 3.81 $\pm$ 0.26 for both chicks and fledglings. The differences for both chick (z-test for difference of means; z =2.52; $P<0.05$), and fledgling production (z=3.94; $P<0.01$) are significant . This difference could have been caused if the experienced females were older, and there was a reproductive advantage to that age.

Figure 5.2 Egg, chick and fledgling production in relation to female Sparrowhawk age in Edinburgh, 1986-1989, including only sites where the number produced was certain.

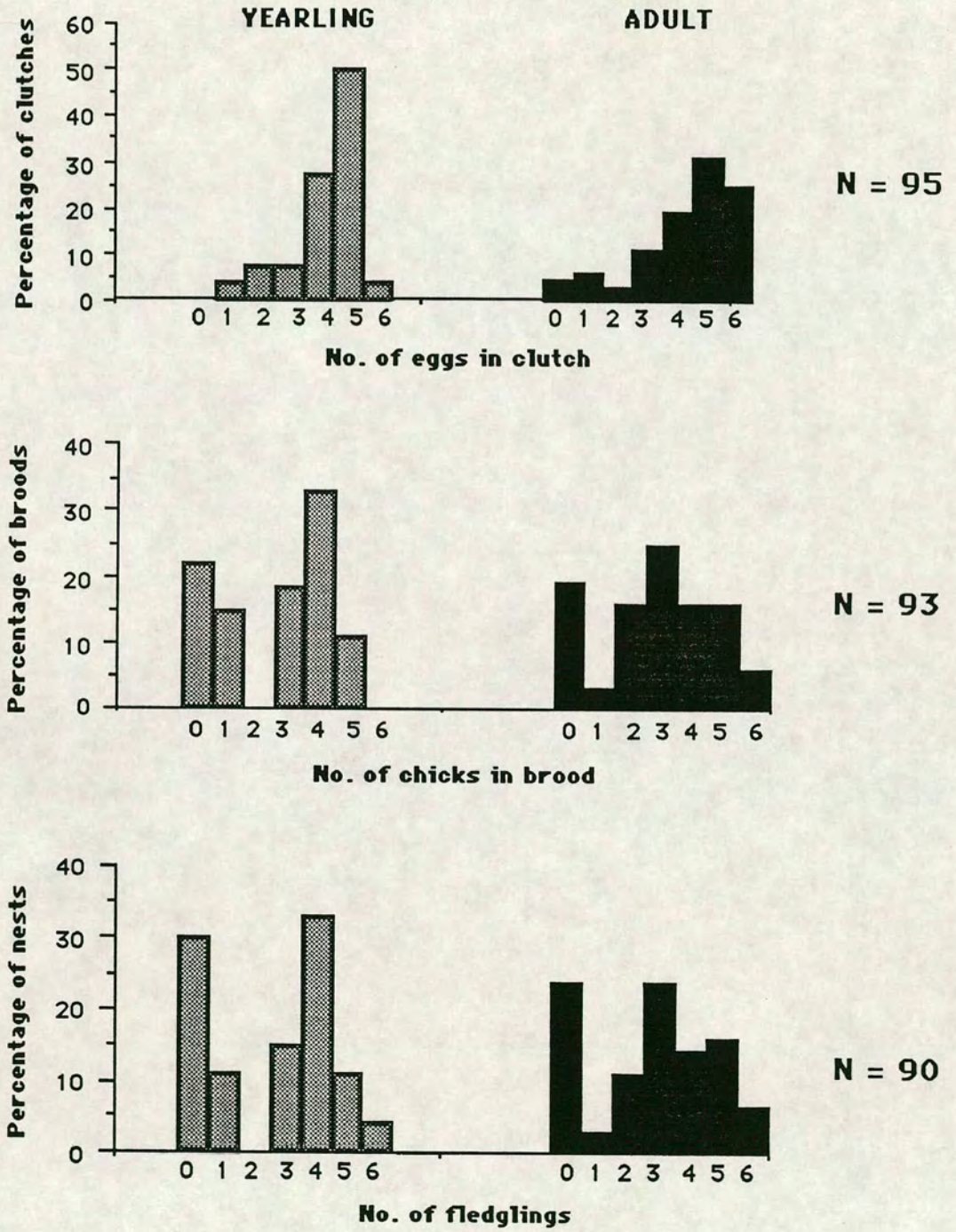


Table 5.3 Production in relation to ages of breeding Sparrowhawks in Edinburgh, 1986-1989. (NA=not applicable)

EGG PRODUCTION

AGE OF BREEDERS	N	MEAN ± S.E.
Adult Male-Adult Female	31	4.42 ± 0.32
Adult Male-Yearling Female	16	4.37 ± 0.27
Yearling Male-Yearling Female	3	4.75 ± 0.25
Yearling Male-Adult Female	0	---

HATCHLING PRODUCTION

AGE OF BREEDERS	N	MEAN ± S.E.
Adult Male-Adult Female	32	3.31 ± 0.35
Adult Male-Yearling Female	16	2.56 ± 0.44
Yearling Male-Yearling Female	3	3.00 ± 1.53
Yearling Male-Adult Female	1	4.00 ± NA

FLEDGLING PRODUCTION

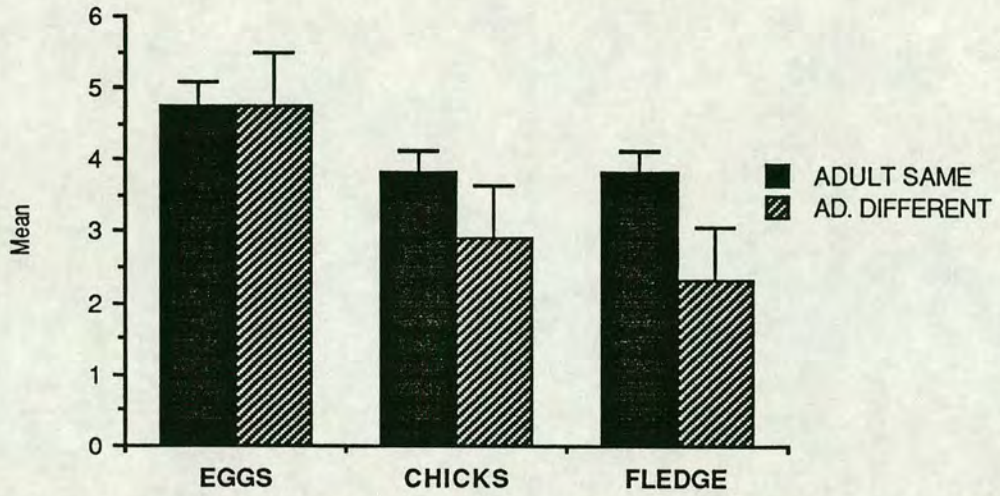
AGE OF BREEDERS	N	MEAN ± S.E.
Adult Male-Adult Female	33	3.48 ± 0.33
Adult Male-Yearling Female	17	2.53 ± 0.40
Yearling Male-Yearling Female	3	3.67 ± 0.88
Yearling Male-Adult Female	1	4.000 ± NA

Table 5.4 Mean clutch size, brood size, and number of fledglings produced in relation to female turnover in Edinburgh, 1986-1989, (N)= number of nests. Females of all ages.

	Eggs		Chicks		Fledglings	
Same Female	4.87±0.29	(15)	3.80±0.38	(16)	3.87±0.35	(16)
Different Female	4.63±0.18	(38)	2.73±0.33	(33)*	2.63±0.33	(38)**

* - z=2.12; P<0.05, ** z= 2.59; P<0.01; z-test for difference of means.

Figure 5.3 Production (mean number per nest + standard error) in relation to adult female Sparrowhawk turnover in Edinburgh, 1986-1989.*



*- Based on 16 instances where the female was the same, and 12 where she was different.

Turnover did not always occur at the same time of year. In most cases in which a breeder was new to a nesting place, the change occurred well before egg-laying. At three nesting places it occurred relatively late in the breeding season, with the bird that ended up breeding replacing a member of an 'established' pair. One replacement was of a male which died, one of a female which died, and one of a female whose fate was unknown. Behavioural details of these replacements are given in Chapter 6. In all, the bird that was replaced was an an adult, and the replacement was a yearling. The production statistics for these three are given in Table 5.5, and do not differ significantly from pairs in which one of the breeders was new.

Table 5.5 Production of Sparrowhawks at three nesting places where the replacement of one of the members of the resident pair occurred late in the breeding season.

Site	Replacement Date	Egg Date	Eggs	Chicks	Fledge
0002	~26/05/87	06/06	4	4	4
0003	~21/05/87	~05/05	0	0	0
0004	~16/04/88	27/05	3	2+	0

5.3.6 Human impact and disturbance

Human impact on Sparrowhawk productivity in Edinburgh was difficult to quantify. Direct human impact included cases in which the nest was robbed or destroyed, the breeders were killed by people (e.g. shooting) or man-made objects (e.g. windows, wires, and cars), or when the level of human activity caused the interruption of brooding. Indirect human impact included the possible effect of pesticide levels on egg hatchability and adult fecundity, the effects of pollution and food subsidies on prey populations, and the impact of habitat changes caused by construction and development.

Of 28 known post-fledging deaths of ringed Sparrowhawks, 5 bred within the city during the study period before dying. Twenty did not survive their first winter, so their contribution to the breeding population was nil. Three were known to have survived more than one year, but did not breed within the study area.

Of birds which died, but were known to have bred, only one was known to have been killed directly by human action. This adult female was shot just prior to egg laying (she was replaced by a yearling, and four chicks were raised.). One adult female with large fledglings was killed when she collided with a window; the fate of the young was unknown. One female was found dead on the nest with three, 8-10 day old chicks dead beneath her. No reason for her death could be determined. The cause of death of the other two breeders was undetermined. Chapter 3 discusses causes of Sparrowhawk mortality.

On four occasions attempts to destroy nests were known to have been made by humans. Three were successful, and a total of 14 eggs were destroyed. Two of the pairs that were affected re-laid, produced 8 eggs, and ultimately 5 fledglings. Four eggs in the other nest were destroyed, and no re-laying occurred.

The effect of disturbance on the ability of the female to incubate eggs and young is harder to assess. Many of the eggs which failed to hatch had small holes in them which may have been caused by the female having to leave quickly due to human disturbance. No assessment of the brooding ability of the female was made. However, the level of human activity had no effect on the overall production of fledglings per nest.

The effects of pollutant levels on production were difficult to evaluate, and were not exclusive to the urban environment. Examination and pesticide analysis was carried out on 24 eggs (Appendix 1, Tables 5.2 and 5.3). In 11 cases the eggshells were cracked or pierced. An index of shell thickness was determined for 21 of the eggs. The index averaged 1.32 ± 0.27. Table 5.6 summarizes the data on egg pollutant levels.

Table 5.6 Mean pollutant residue levels (ppm ± S.E.) found in Sparrowhawk eggs in Edinburgh, 1986-1989.

Pollutant	No of eggs w/ detectable levels of pollutant	Pollutant level (Mean + S.E.)
HCH	1	0.08
HCB	3	0.14 ±0.03
HEOD	17	1.13 ± 0.18
DDE	17	4.51 ± 0.83
PCB	17	18.32 ± 2.78
Mercury (Hg)	17	0.52 ± 0.07
HE	8	0.46 ± 0.04

Pollutants were not found in very high levels in any of the eggs. Only a few eggs displayed a level significantly different from the others examined in this study . The two highest values of DDE, 13.05 and 13.47 were from eggs laid at very different nesting places (An inner-city cemetery, and a conifer plantation in an essentially rural setting on the edge of the city), and were significantly different from the rest of the eggs examined (Dixon's test for outliers; r_{22} (for both) > 0.739, $P < 0.01$). The egg from the city nest with the high level of DDE also had the highest level of PCB's and the second highest level of Mercury.

No relationship was apparent between production and residue level. Even in the clutches where the levels of toxins seemed high, no reduction in actual productivity for the nesting place was apparent. However, the nesting places at which the most contaminated corpse (Chapter 3) was found, and the one at which the most contaminated egg was laid and from which the most PCB contaminated male corpse came, were only 1.2 km. apart in the centre of the city. Although both of these nesting places were occupied in all years of the study by birds which always produced eggs, the effect of human disturbance on them, whether in the form of direct persecution or elevated contaminant levels was most obvious. Between these two nesting places, besides the aforementioned corpses, another, unanalysed, corpse was found. One nest with chicks was abandoned, although neither of the adults died (See above). At these

two nesting places over the study period, two nests were destroyed by humans with the loss of 9 eggs; new nests were built, and 7 eggs were laid, 6 chicks were produced. One clutch was destroyed (4 eggs), and no re-nesting occurred. One nest tree was girdled in an apparent attempt to affect the Sparrowhawks. Further, in adjacent nesting places, another corpse was found (shot), one nest failed for unknown reasons after two eggs were laid (and were subsequently eaten by squirrels), and turnover was high for females (75%).

5.4 Discussion

Edinburgh contains many woodland areas (Chapter 1). All urban woodland areas, irrespective of structure or proximity to human disturbance or other Sparrowhawk nests, were used by Sparrowhawks, both breeders and non-breeders, throughout the year. Woodland areas which seemed ideal for nesting, but in which no nesting occurred, were nevertheless used extensively by both breeding and non-breeding birds as places to hunt, loaf, and roost.

Sparrowhawks, although dependent upon woodland for nesting, are selective in their choice (Newton 1986). Areas which are too dense, or too open are generally unacceptable for nesting, but are used by the Sparrowhawks while hunting and roosting (Chapter 4). The parameters examined in this study which described the nesting habitat of the Sparrowhawk, were similar to those examined by Newton in more rural areas. However, it was difficult to describe some nesting places as being situated in a 'wood', since the trees in some parks and in the fractured habitat of private and public gardens were separated by relatively large distances. A better description of these nesting places might be 'single trees'.

The composition of woodlands in which Sparrowhawks chose to nest varied greatly. Mixed woodland, wholly broad-leaved, and wholly coniferous woodlands were used. These woodlands varied in size, and were not entirely comparable with the rural situation, since Edinburgh had only one extensive stand (covering 81 hectares). The complexity of the undercover varied from mown lawns to highly diverse communities of shrubs, small trees, ferns, and grasses.

Although there were few large tracts of mature, mixed woodland within the city, the largest (mixed or otherwise), never had as many successful nest places as would have been expected from its size, and the mean nearest-neighbour distance (Chapter

3) within the city. Reduction in the occupation rate due to the over-maturity of the woodland is a phenomenon found elsewhere in the studies of Newton (1986) and Petty (1979).

In some wooded areas nesting was not found, but was expected. However, human use of the woodland did not seem to have a great effect on whether or not a site was occupied since two of the city's most highly-used gardens, the Royal Botanic Gardens and Prince's Street Gardens were regular nesting places. A longer term assessment of the effects of human disturbance on the different stages of production may reveal some effect.

Within woodlands which were chosen for nesting by Sparrowhawks, the location and placement of the nest was to a certain extent predictable, and similar to Sparrowhawks elsewhere (Newton 1986; Petty 1979; Wyllie pers. comm.). Comparisons with North American congenors reveal Sparrowhawk nest characteristics are most similar to those of the Sharp-shinned Hawk (*Accipiter striatus*) (Platt 1976; Jones 1974; Reynolds *et al.* 1982).

Warkentin and James (1988) in their study of urban, tree nesting Merlins in Saskatoon, Canada investigated nest site selection. Since Merlins, like other falcons, do not build their own nests, and in the case of the Saskatoon population, nest in disused Corvid nests, the results are not strictly comparable with the Edinburgh Sparrowhawks. However, the Merlins did prefer nests located in conifers over those in broad-leaved trees, and the nests they selected (usually Crow, *Corvus brachyrhynchos*) were about two-thirds of the way up the tree, despite the fact that Crows often build their nest higher in the tree. These characteristics of nest placement seem advantageous in concealing the nests from both ground and aerial predators. Measures of human disturbance, tree height and circumference, and assessments of the complexity of the woodland occupied by the Merlins seemed unimportant to nest site/place selection given the range of woodlands available in Saskatoon, a characteristic shared with the Sparrowhawks of Edinburgh.

In other raptorial species it has been shown that interspecific competition for a nesting places might affect the occupancy of a place by a particular species (e.g. Schipper 1978; Bomholt 1981; Titus and Mosher 1981; Reynolds, *et al.* 1982; Green and Morrison 1983; Schmutz, *et al.* 1980; Village 1990). Perhaps city Sparrowhawks suffered from some sort of competition with other birds. Where

large numbers of Rooks *(C. frugilegus)* nested, no Sparrowhawks were found, although in other respects the woods seemed favourable. Sparrowhawks did nest in the same woodlands as non-colonial Corvids -- Magpies *(Pica pica)* and Crows *(C. corone)*, and egg predation by Corvids might have reduced nestling production at such nesting places.

No exclusion by Kestrels *(Falco tinnunculus)* was apparent either. In some woods only Sparrowhawks or Kestrels were found, while in others both bred successfully. Since urban Kestrels depend on avian prey to a larger extent than their rural counterparts (Crichton 1977, Yalden 1980, Pikula *et al.* 1984), they might compete with Sparrowhawks for the same food. Local bird watchers have told me that Edinburgh Kestrel numbers are diminishing, but if this is due to competition with Sparrowhawks, I have no evidence. The ability of the Kestrel to utilize buildings and cavities as nest sites, means they do not compete directly with Sparrowhawks for nesting sites.

Another predator/competitor which might have affected the number, distribution, or breeding of Sparrowhawk was the Tawny Owl (*Strix aluco*). In virtually all of the Edinburgh Sparrowhawk nesting places, a pair of Tawny Owls also bred. Although Tawny Owls are known to prey upon Sparrowhawks (Newton 1986), no evidence of this was noted in Edinburgh. Ninety-three percent of the diet of Tawny Owls in London has been reported as being avian (Bevan 1965, 1982). Casual examination of the contents of owl pellets found on Edinburgh Sparrowhawk sites confirmed that Tawny Owls utilize at least part of the same food resource as Sparrowhawks. Since the Tawny Owl nests either in a cavity or upon an old nest, direct conflict for nesting with the Sparrowhawk is minimal. The possibility of competition between urban Sparrowhawks and both Kestrels and Tawny Owls for food merits further investigation, as does their predation upon Sparrowhawk chicks.

Environmental conditions and individual characteristics both play a part in determining the reproductive success of individual Sparrowhawks, both within a season and over the longer term. The common denominator in most of these factors is food; although predation, pollution, and accidental mortality could also have an impact (Newton 1986). In other raptors, too, production measures seem to be most closely linked to prey availability (For review: Beecham and Kochert 1975; also: Cavé 1968; Gargett 1977; Newton 1989 b; Wikman and Linden 1981; Watson and Langslow 1989). The production statistics in Sparrowhawks are no exception (Moss

1976, 1979; Petty 1979; Geer 1981; Newton 1976 a, b, 1986; Newton and Marquiss 1981, 1982 a, 1984, 1986; Newton, *et al.* 1986).

Occupancy, as defined by the number of nest sites in which at least a nest structure was started in any year, remained fairly constant. Stability of this nature in the southern Scottish population studied by Newton (1988) was attributed, to a large extent, to spacing behaviour, coupled with density-dependent losses in the pre-breeding subset of the population (Chapter 3).

In most respects my findings were consistent with those of longer term studies in rural areas (Newton 1986). A high percentage of nesting places were utilized by Sparrowhawks in the pre-breeding season, January-April, and over 50% of the known, recently used places had nests over the study period. Some were occupied in all years of the study, others less often. Some places which had old nests from years prior to the study went unoccupied during the study. Many more places were used by potential breeding pairs in late winter, but their breeding effort ended before a nest structure was started. The egg, chick, and fledgling production means were slightly lower than in Petty's (1979) area, but were within the range of values from 1972-1984 reported by Newton (1986) in southern Scotland. The mean number of chicks in the urban Sparrowhawk population in Prague, Czechoslovakia was 3.12 $\pm$ 0.1 (Peske 1987 and pers. comm.), not significantly higher than in Edinburgh (Unpaired t-test (two tailed); t= -1.998, P=0.08, NS). The most common size of clutch, brood and number of fledglings was the same in Edinburgh as in the other studies (Newton 1986), and the equal sex ratio at fledging was similar to the findings of Newton and Marquiss (1979). The high survival of hatchlings of both sexes in the city was probably due to the plentiful prey (Chapter 2)(Moss 1976).

The productivity of other urban raptor populations seems to be unaffected by living in cities (e.g. Oliphant and Haug 1985; Gennaro 1986), and in some cases this extreme environment provides new opportunities for some predatory species (Craighead & Craighead 1956). In all the measures of success examined here, the Sparrowhawk in Edinburgh is as productive as its rural counterpart. Other important statistics of production, such as life-time reproductive output, might differ from those found in the Sparrowhawk population of southern Scotland (Newton 1985, 1986, 1988) due to mortality differences (Chapter 3), but were untested in this study.

The affect that cuckoldry has on the production of Sparrowhawks is not clear. Sparrowhawks do engage in extra-pair copulations, and the female is able to store sperm for an undetermined amount of time (Chapter 6). In Edinburgh, Sparrowhawk offspring are produced that are not related to the male holding that particular nesting territory late in the nesting season. If the 5% of tested individuals found to be products of cuckoldry in this study are representative of the population as a whole, it would mean that during this study over 10 chicks were produced from matings between a resident female and a male different from the one identified as her mate. In this study it was not very likely that the resident male was misidentified, because they were all colour marked, and being observed frequently for behavioural studies.

The results of the paternity checks conducted on the Edinburgh Sparrowhawks shall be examined with those carried out on Sparrowhawks elsewhere in Britain, where cuckoldry has also been found (Newton pers. comm.). The data were not complete enough to determine whether neighbouring males were favoured as cuckolds, or whether paired males were more likely to produce extra-pair offspring than were non-territory holders (Chapter 6). The likelihood of chicks resulting from extra-pair copulations making it into the breeding population could not be assessed in this study.

The effects of age and experience of the breeders, the weather, and the impact of human influences, including pollution were examined. In raptorial birds the effects of weather on production occur throughout the year, not only on the raptor itself, but also on prey species (Biggs, *et al.* 1984; Kostrzewa 1989). For Sparrowhawks a link between weather and annual population changes has been shown (Newton and Marquiss 1986). If bad weather affects either prey levels or the ability of the raptor to hunt, the females are not able to gain the weight needed to attempt to nest. Weather can influence the date of laying (and in general clutches laid earlier are more successful) (Sparrowhawks: Newton and Marquiss 1984; Peregrine Falcons: Olsen and Olsen 1989 a). It can affect the hatchability of eggs, and the survivability of chicks to fledging age (e.g. Court *et al.* 1988; Olsen and Olsen 1989b). Indirectly, if the spring and summer are cold and wet, the amount of prey that will be available to a bird of prey in the subsequent autumn and winter may be low, and mortality high (Newton 1979).

Early spring weather influenced Sparrowhawk production: cold, wet weather in

Edinburgh in February-April reduced the number of nests, eggs, chicks and fledglings produced, a situation similar to that found by Newton and Marquiss (1986).

Once eggs are produced, not only can wet weather reduce the ability of the adults to hunt, but cold, wet weather can cause mortality through the chilling of nestlings (Moss 1979; Newton 1979). In Moss' study (1979) causes of nestling mortality were starvation, wet weather, predation, and desertion in order of importance. The fact that in Edinburgh, in only the warmest and driest years were clutches of 6 raised to fledging may illustrate an increased ability of the parents to feed large broods in good years. Generally, the data relating weather to production are also consistent with the findings of Geer (1981) and Newton and Marquiss (1984) for Sparrowhawk, Kostrzewa (1989) for Honey Buzzard *(Pernis apivorous)*, Davis and Newton (1981) for Red Kite *(Milvus milvus)* and Olsen & Olsen (1989 a and b), and Mearns & Newton (1984) for Peregrine Falcon *(F. peregrinus)*. Temperature effects on the urban Sparrowhawk population were less obvious.

In Edinburgh the age and experience of the members of the pair was examined, as was its effect on the reproductive output of the individuals. Adult females produced on average more fledglings per productive nest than did yearlings, similar to findings of Newton (1976). Other measures of reproduction, eggs/nest and chicks/nest, were not different in adults and yearling females in the city. In studies on other species of raptor, the difference between the productivity of yearlings and that of adults is variable (Hammerstrom 1969; Hickey and Anderson 1969; Newton, *et al.* 1981; Village 1990). The effect of male age and experience could not be closely examined since relatively few yearlings bred in the city.

Breeders of both sexes were usually in adult plumage. On average, pairs made up of an adult male and an adult female produced more eggs, chicks and fledglings than did any other pairings. Also, a higher percentage of the eggs produced by adult-adult pairs produced fledglings. This agrees with studies of Sparrowhawks and Kestrels (*F. tinnunculus*) in southern Scotland (Newton *et al.* 1981, 1984, Village 1980, 1990).

The site-experience of the members of breeding pairs and its effect on production was investigated. Among adult females, birds that remained on a site in consecutive years produced more chicks and fledglings. On a larger sample, Newton and Marquiss

(1982 a) found that the mean laying-dates of pairs that had not changed site were significantly earlier than those of pairs in which the female was new to the site.

Human disturbance, whether direct (e.g. Richmond 1959; Bijleveld 1974; White 1974) or indirect (e.g. Ratcliffe 1967; Hickey and Anderson 1968; Cooke 1973, 1979; Newton and Bogan 1974, 1978; Newton 1979; Voous 1977) has been documented as having an effect in many raptorial species in many countries. For the most part, the effect of human activities has been negative (Van der Zande, *et al.* 1984), although in some situations it has been positive (e.g. Craighead and Craighead 1956; Gennaro 1988), with populations expanding in areas of human habitat modification. In some parts of Europe the Sparrowhawk population has grown in parallel with the maturation of stands of conifers, planted after World War II.

Historically in Britain, the direct persecution of the Sparrowhawk was due largely to the perception of them (and other raptors) as vermin (Ash 1960; Moore 1957; Newton 1972, 1979, 1986), for which they were shot, poisoned, trapped, and had their nests destroyed. Egg collecting as a hobby also had some minor effect on reproductive success. In Edinburgh, free-flying Sparrowhawks were killed and injured by humans (Chapter 3). Also, nests containing eggs or chicks were destroyed. In some cases these incidents were accidental, in others deliberate. The motivation for deliberate disturbance was unknown, but at one site racing pigeons were being raised in close proximity. The effect of direct persecution and human disturbance on production could not easily be assessed over the short term of this study, particularly since the impact of the disturbances was offset by re-nesting, and/or replacement of the breeders.

Indirectly, Sparrowhawk numbers were probably supported by the human feeding of prey birds (Chapter 2). Sparrowhawks were seen on numerous occasions preying upon birds that were feeding on garden bird-tables or being fed by members of the public in the gardens and parks of the city. They were also seen using buildings and other man-made objects for concealment when hunting. It is not unusual that human habitat modification has led to certain areas becoming more suited to certain species of raptor than others, but the majority of these situations remain primarily rural. The behavioural modifications required to not only hunt, but reproduce successfully in the city are demonstrably available to them. Only in a relatively few situations, such as Merlins in Saskatoon (Oliphant and Haug 1985), Kestrels in the cities of Europe (Village 1990) and Asia (Y. Leshem pers. comm.), Mississippi Kites

(Gennaro 1988) in North America, and scavengers (e.g. Black Kite, *Milvus migrans*) of the cities of Africa and India, are good populations of diurnal raptors living and breeding in urban environments.

Levels of pesticides and pollutants, particularly organochlorines, have been shown to have an effect on the productivity of birds, particularly raptors (e.g. Ratcliffe 1967, 1970; Hickey and Anderson 1968; Cooke, *et al.* 1982; Section 5 in Cade, *et al.* 1988), including Sparrowhawks (Newton 1972 and 1973; Newton *et al.* 1979). High levels of these pesticides were found in the eggs of Sparrowhawks collected in south Scotland in 1971 (Newton 1973); these eggs suffered a high rate of shell thinning, egg breakage, and embryonic death. In the city, the levels of pollutants in the unhatched eggs of birds breeding in the study area, and in the corpses of birds found dead (Chapter 3) although highly variable, were not of the level to have caused significant negative effects. The relatively few eggs and corpses that were available for analysis did not provide any conclusive results concerning the impact of contaminants on Sparrowhawks in the urban environment. The variables used in this study as indicators of human disturbance may not be sensitive enough to reveal effects on production.

Newton (1986) showed that indirect human disturbances which caused the death of individuals, desertion of nest sites, and a reduction in reproductive output does occur in the countryside. The most obvious negative human impact on the city Sparrowhawks in the long term will probably be the destruction of nesting habitat due to building and development.

CHAPTER 6

Breeding Behaviour

6.1 Introduction

Few studies have been made of the behaviour of forest-dwelling raptorial birds. Because most species are shy and range over relatively large areas, only casual observations have been made of nesting birds.

The Sparrowhawk is one of the most extensively studied raptors in the world, but the details of its behaviour away from the nest have yet to be thoroughly examined. Owen (1916-1922) and Newton (1986) reported some of the breeding behaviour. Radio-telemetry has allowed their hunting, roosting, and ranging behaviours to be studied (Marquiss and Newton 1982). Still, most behaviours have been only casually observed during field work aimed at understanding other aspects of the Sparrowhawk's ecology (See: Brown and Amadon 1968, Brown 1976; Cramp and Simmons 1980; and Newton 1986)

In Edinburgh, Sparrowhawks have become accustomed to living in close contact with humans, and can be easily approached. This 'tameness', along with the relative openness of the urban nesting places, allowed close observation of behaviours .

Sparrowhawks rear only one brood each year, and their mean life-span is relatively short (Chapter 5). As for any animal, it is important for them to maximize production of offspring by any means possible. Although the breeding pair is the annual functional reproductive unit, the sexes pursue separate reproductive strategies which enhance individual reproductive success.

This chapter investigates the spring-time behaviour of breeding Sparrowhawks (some observations of non-breeders were also made), in order to define the reproductive strategies of both individuals and the pair. Although behavioural observations were made primarily at highly productive nesting places, the behavioural variability among individuals and pairs was analysed to investigate the variation in reproductive success (Chapter 5). Useful to this analysis was the replacement at 3

nesting places of adult breeders by yearlings. The inter-relatedness of breeding behaviours was also examined.

6.2 Methods

An effort was made to colour and/or radio-mark (Chapter 1) all the birds (both breeding and non-breeding) within an area in which paired Sparrowhawks were known to be particularly observable (north Edinburgh, Appendix 2, Figure 4.2).

Observations were made at 23 Sparrowhawk nesting places starting in early February in 1987-1989. In 1987, 42% of the breeders at the nesting places under observation were individually recognizable, in 1988, 63%, and in 1989, 89%. In addition, some of the non-breeders were also marked and could be recognized in all of the years. Similar proportions of male and female breeders were able to be identified in each year.

Observations continued until 7-10 days after egg laying or until failure was obvious. The latest observations were in early June. Nesting places were selected randomly (by assigning each a number and using dice) for specific observation bouts with occasional modification for practical considerations, such as human disturbance. Observation bouts usually lasted at least two hours, some lasted 8 hours. The longer observation bouts were useful to confirm the context in which the individual component behaviours were set. Table 6.1 details observation activity.

Table 6.1 Details of observations made of Sparrowhawk breeding behaviour in Edinburgh, 1987-1989.

Year	Observation Period	No. of Sites*	No. of Bouts	Total Hours
1987	5 Feb.-23 May	6	84	217.2
1988	7 Feb.-11 June	8	132	480.5
1989	4 Feb.- 2 June	9	109	427.0

* Some nesting places were studied in more than one year, some were occupied by the same breeders in more than one year. Number of hours of observation per site was variable.

Behavioural observations were made using binoculars (10 X 40), and were recorded on a small tape recorder. Notes on weather were also made. At the end of the day, recordings were transcribed.

Sixty types of breeding behaviour by Sparrowhawks were identified and recorded in the field using a modification of Walter's (1983) 'actigram' (Appendix 1, Table 6.1). For this chapter a subset of these behaviours (nest building, copulation, feeding, display and defense, and attendance at the nesting place) are dealt with in more detail.

Observations focused on the pair, and were probably biased toward well established pairs. Observations of non-breeders, poor breeders, and late breeders were also made. Some non-breeders and replacement breeders were radio- and/or colour-marked. At some nesting places, extra-pair individuals were sometimes involved in nearly all types of breeding behaviour. Some of these were colour- and/or radio-marked. These individuals were sometimes established breeders at other nesting places.

As far as was possible, time, duration, weather conditions, and the identity of the bird was recorded for each behaviour observed. Birds seemed more active during dry, warm weather, particularly in the 2-3 weeks prior to egg laying. Observations were made in all types of weather. Some behaviours, such as 'nest building' were easily separated from others, while some (e.g. vocalizations) were difficult to characterize.

Copulation attempts and feeding behaviour were calculated as rates (frequency of occurrence). Nesting place attendance was expressed as the proportion of the observation time the bird(s) was in attendance at the nesting place.

To minimize the variation caused by weather, data from all three years were pooled. Generally, all hours of observation were used to calculate seasonal variation in behavioural rates, whereas daily variation in behavioural rates was determined from observations made in complete hour intervals. The hours spent observing replacement events were not included in the calculation of behavioural rates for the population of long established breeders (See below). These criteria result in what are probably conservative estimates of rates and total number of occurrences of

certain behaviours.

Since the pairs studied did not lay eggs on the same Julian date, seasonal variation in behaviour was examined relative to egg date (Egg date=0). Since day length was increasing as spring progressed, diurnal variation in behaviours was studied relative to sunrise (Sunrise=0). The changing speed with which the sun rose and set throughout the spring also affected the amount of time before sunrise and after sunset in which there was enough light to carry out behavioural observations.

Nest building and display/defense are treated differently since they were not so much events, but assemblages of behaviours which, within themselves, were highly variable. Variation in nest building effort was probably partly dependent on the structure of the nesting place itself (type and spacing of trees, etc.), whether it was the renovation of an old nest, or the building of a completely new nest, and the date of pair establishment (Newton 1986).

Defensive displays may have been influenced by the size of the urban Sparrowhawk population, and the breeding density in a particular area. Only a small subset of the display behaviours observed could be used, since I was not always sure of the motivation for display. In some instances, display was probably a form of advertisement for a mate, in other situations it was used to warn competing birds that a nesting place was occupied. It probably also served in cementing the pair-bond (Newton 1979).

No attempt to analyse vocalizations was made. Vocalizations associated with the breeding behaviours are described in the appropriate section if they were different from those described elsewhere. The terminology for these, as much as is practical, follows the review by Cramp and Simmons (1980).

As far as is possible, participation in breeding behaviours by extra-pair individuals (intruders) is discussed in each behavioural section. Intrusive behaviour by non-pair individuals (either non-breeding or breeding at another place) is discussed in light of the defensive reaction of established pairs. Roosting at nesting places by birds which were not nesting there as an aspect of intrusive behaviour is discussed in Chapter 4. Non-breeding intruders are assumed to represent the non-breeding population as a whole. Although some of the unmarked intruders within the area might have bred, and some of the marked birds may have moved elsewhere to breed,

this is probably not true for many of them.

Observations of extra-pair copulations (EPC's) are presented separately from those of copulations between members of an established pair. They are defined as copulations occurring between a member of an established breeding pair, and any other Sparrowhawk that is not its partner (Chapter 1). All copulations which could not be distinguished as being either extra-pair or between members of an established pair (i.e. during replacement of an established breeder) were excluded from analysis.

Two yearling females in the middle of their laying sequence were examined for sperm storage tubules (SST's). One was caught in the late evening, one in the early morning. These individuals were sacrificed. Their reproductive tracts were removed, and placed in phosphate buffered saline buffer, and dissected under a dissecting microscope. The walls of the reproductive tract in Sparrowhawks are pleated and muscular to aid in the accommodation and expulsion of the egg. The connective tissue associated with the pleats was removed using very fine scissors, scalpels, and forceps---instruments designed for ocular surgery were ideal. After the connective tissue was removed, and the reproductive tract was pinned out on a piece of cork submerged in the buffered saline solution, it was examined systematically with a dissection scope for SST's. In the event the SST's were very difficult to spot, and were easiest to distinguish when they actually held sperm. Dr. Tim Birkhead, of Sheffield University, who has had experience in the examination of SST's in many species did the examination, and confirmed that the structures observed were indeed SST's. The numbers of SST's within the reproductive tract and number of sperm stored within were counted. Post-surgery, preliminary histological preparations were made. Plates 6.1 a and b are these preparations.

Data collected at the 3 places where an established breeder (resident) was replaced by a hitherto un-established bird (replacement), are presented in each behavioural section. Where appropriate, they are compared to the behaviours of long-established pairs. In all three, adults were replaced by yearlings. In one the male died (Dean, site 0004, 1988). In another, a female whose fate was unknown (Fettes, site 0003, 1987) was replaced. In the third, the female was shot (Warriston, site 0002, 1987).

These situations were not easily compared since they occurred both at different times in the spring (two occurred in April, one in May-June), and in different years.

Also, the reproductive condition of both the replaced and replacement birds and their mates could not be estimated since these events occurred at different times relative to both egg-date and mean egg-date of the urban population in that year. The replacement of breeders which were known to have died occurred within a few days, so the variation in behaviour of the pair prior to the replacement could not be tested for most behaviours. Where feasible, behaviours of Sparrowhawks involved in a replacement event are analysed and compared to those of long-established pairs. For some behaviours it was possible to examine the variation in behaviours of individuals before and after replacement.

6.3 Results

6.3.1 Nest building

Nests and nest building behaviour, dates of initiation, and time taken to build were highly variable between nesting places, but did not differ greatly from the description by Newton (1986). Some new nests were started as early as November, some in May. Some were large and newly built, others were little more than renovations of old nests (of Sparrowhawks, Corvids, and squirrels). Nests that were destroyed were often replaced by new nests which could be finished within a few days. Some nests were virtually complete weeks before eggs were laid. I could not determine which sex chose the nesting site. As explained later, males initiated many of the nesting bouts, but females brought larger twigs. The first twigs of the nest are generally larger than those added nearer to its completion. 'Inspections' and 'twig-carrying behaviour' as described by Newton (1986) were seen in Edinburgh Sparrowhawks.

The twigs used in nest construction reflected the composition of the woodland, larch twigs seemingly being favoured. Of three nests from nesting places located in mixed woodland where larch, pine and broad-leaved trees were available, almost 90% (>90% of weight) of the sticks used were larch. In wholly broad-leaved woods, or wholly coniferous woods, the nests were constructed from twigs of those trees solely. Three nests which were freshly built in 1988, and in which chicks were successfully reared to fledging, contained 600-800 twigs, and weighed (dry) around a kilogramme. These appeared to be 'average'-sized nests. Newton (pers. comm.) has counted as many as 1500 twigs per nest

Usually, building by either member of the pair was done in the presence of their mate, but at times one would build while the other was absent. Sometimes birds called as they carried material to the nest, but the amount of calling varied between and within individuals, and days. The call was similar to that used by the female when food begging, but was usually shorter and the inflection on the second half of the call was not as obvious.

Twigs were usually clipped from a tree with the bill, but four different females were observed breaking off larger branches with their talons. Some males were observed hanging from twigs which did not break off easily. Building material was usually carried in the talons, but the bill was also used. Some building material was chosen from the ground. Occasionally, Sparrowhawks would go to the nest with no building material. It was rare to see both birds on the nest at once. If they were building together, one usually vacated the nest as the other alighted.

The variability in nest building behaviours between pairs of Sparrowhawks made the calculation of seasonal or daily rates difficult. Since the number of observation hours in the morning was not equal to the number of observation hours in the afternoon, the nest building bout counts were corrected for this difference. Most nest building (73%) occurred in April, but whether this activity was tied to the Julian date or the egg date, could not be determined. Within the day, nest building occurred between 0410 hrs and 1926 hrs (From one hour before sunrise to 15 hours after). Most building, 92%, occurred in the morning.

The female did the bulk of the building. Also, she seemed to bring the largest of the sticks to the nest, presumably due to her larger size. Male Sparrowhawks initiated (carried the first twig to the nest in a building bout) most of the bouts, but made significantly fewer trips to the nest per nest building bout than females (Unpaired t-test (2-tailed): $t = 3.41$, $P < 0.01$). Bouts of nest building by the male lasted between 0.5-25 min. Calculations using the percentage of male and female participation, the number of twigs/nest, and the mean duration of nest building bouts indicate that the nests which were measured and weighed would have taken 39 - 52 hours to build. Table 6.2 summarizes the nest building behaviour of the Edinburgh Sparrowhawks.

Table 6.2 Nest building behaviour of Sparrowhawks in Edinburgh 1987-1989.

	Percentage of bouts initiated (N=336)	Percentage of trips to nest (N=623)	Trips/bout	Mean bout length (min ± S.E.)
Male	64	17	1 - 16	1.6 ± 0.3
Female	36	83	1 - 30+	4.4 ± 2.4

On three occasions at two nesting places, extra-pair female Sparrowhawks added sticks to the nest. In each case, the 'building' was done without the male initiating the bout, and at one of the places the resident female was replaced within a week by the intruder which did the building. In that case, the fate of the original female breeder was unknown. On one occasion an intruding yearling male carried twigs to a disused nest structure at a nesting place where the resident female was present. The resident male was not present, and the female did not react to the intruder.

When a replacement bird occupied a vacant place in the breeding population, the amount of nest building undertaken by the new pair was highly variable, depending on the amount of time before egg-laying, and completeness of the nest built by the original pair. Females which lost their mate continued nest-building during the few days when there was no partner, unlike in removal experiments by Newton *et al.* (pers. comm.).

Table 6.3 describes the relationship between nest building behaviour and copulation, and between nest building and food presentation. The relationships were similar, and non-random. Many nest building bouts occurred immediately after either of these behaviours, but some occurred as much as 3 hours later. Some biases were present. Sometimes the male started to build while the female fed, so starting of bouts initiated by the female might have been influenced by whether or not she had been feeding. If the male had started to build as she fed, the female would usually join in after finishing.

Table 6.3 Relationship between nest building behaviour and other breeding behaviours in Sparrowhawks in Edinburgh 1987-1989

Behaviour	N	Mean time to start of nest building (± S.E.)	% of nest-building bouts occurring w/in 5 min.
Food presentation	106	45±13.8	16 *
Copulation	80	30 ± 11.8	50**

* D = 0.109, P < 0.05; **D = 0.102, P < 0.01, Kolmogorov-Smirnov test for intrinsic hypotheses. Both follow negative binomial (non-random) frequency distributions.

6.3.2 Nesting place attendance/defense

6.3.2.1 Daily variation

Daily variation in nesting place attendance by the members of the pair was determined from 1039 complete hours of observation. Data was arranged relative to sunrise since day-length changed from about 8 hours when observations started in January to about 16 hours in early June when they finished. Sunrise varied from around 0800 hrs to 0350 hrs, sunset from about 1600 hrs to 2000 hrs. A line describing a third order, polynomial equation which best fits the data is drawn to suggest graphically the relationship between time of day and rate of nesting place attendance. No statistical analysis was undertaken using this computed line.

Male Sparrowhawk attendance at the nesting place decreased significantly from morning-time. (Spearman Rank Correlation (two-tailed); N=20, R=0.62; P < 0.02)(Figure 6.1).

Female Sparrowhawk attendance at the nesting place also decreased significantly through the day, although the difference was not as obvious as in the male (Spearman Rank Correlation (two-tailed); N= 20, R=0.56; P < 0.02)(Figure 6.2).

Although both male and female Sparrowhawks spent more of their time at the nesting place in the morning, they were not necessarily there at the same time. Spar-

rowhawk pairs did not spend more time together at the nesting place in the morning than at other times (Spearman Rank Correlation (two-tailed); N=20, R=0.42, NS)(Figure 6.3).

Figure 6.1 Diurnal variation in male Sparrowhawk nesting place attendance (as a percentage of total observation time) during the pre-laying period in Edinburgh, 1986-1989. (Line = calculated polynomial 'best fit').

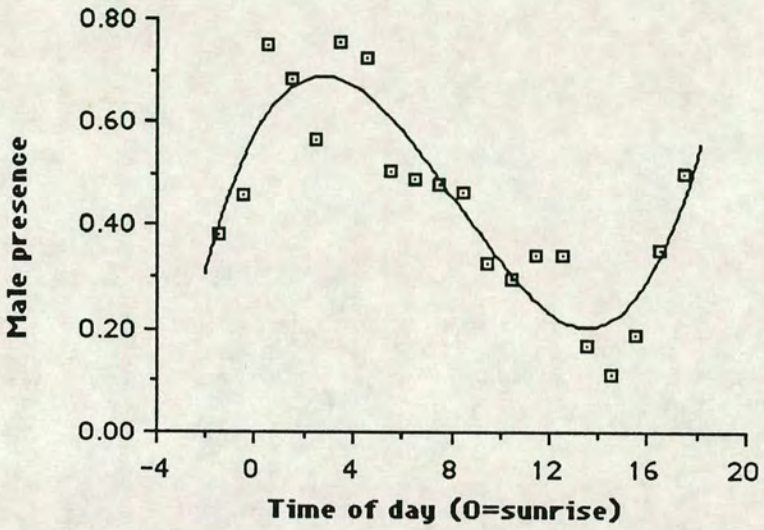


Figure 6.2 Diurnal variation in female Sparrowhawk nesting place attendance (as a percentage of total observation time) during the pre-laying period in Edinburgh, 1986-1989. (Line = calculated polynomial 'best fit').

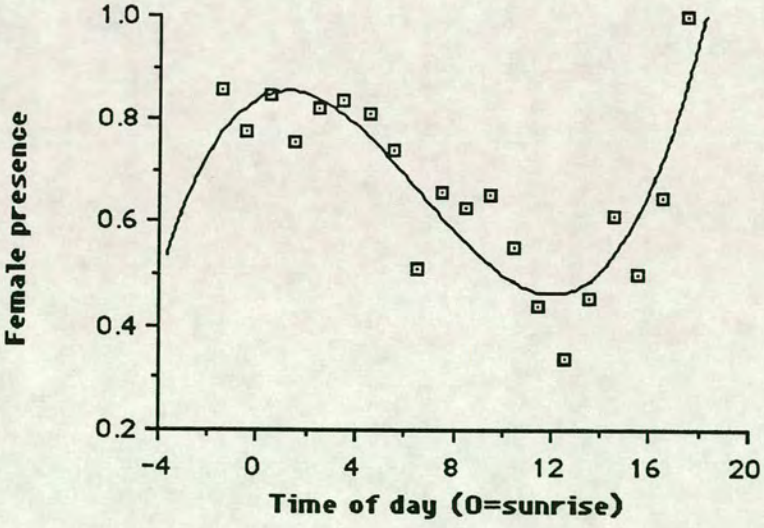


Figure 6.3 Diurnal variation in simultaneous nesting place attendance (as a percentage of the total observation time)by both members of breeding Sparrowhawk pairs in the pre-laying period in Edinburgh, 1986-1988. (Line = calculated polynomial 'best fit').

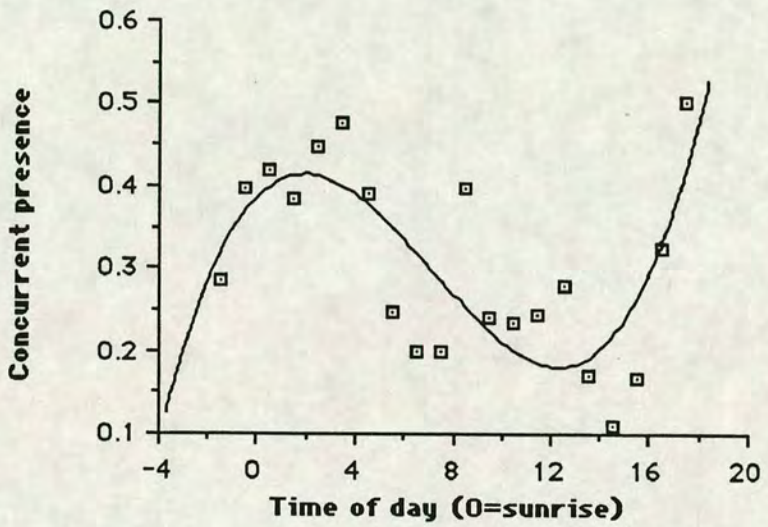


Figure 6.3 suggests that the increase in pair presence in the evening might be related to the generally higher amount of time spent together in the morning (relative to the afternoon). If the data is 'wrapped', concurrent nesting place attendance decreases significantly from 16 hours after sunrise in one day through to 16 hrs after sunrise in the next day (Spearman Rank correlation (two-tailed); N=20, R=0.75; $P < 0.02$). This suggests an effect probably caused by both members of a breeding pair coming to establish their primary roosts at the nesting place, particularly as egg-date approaches.

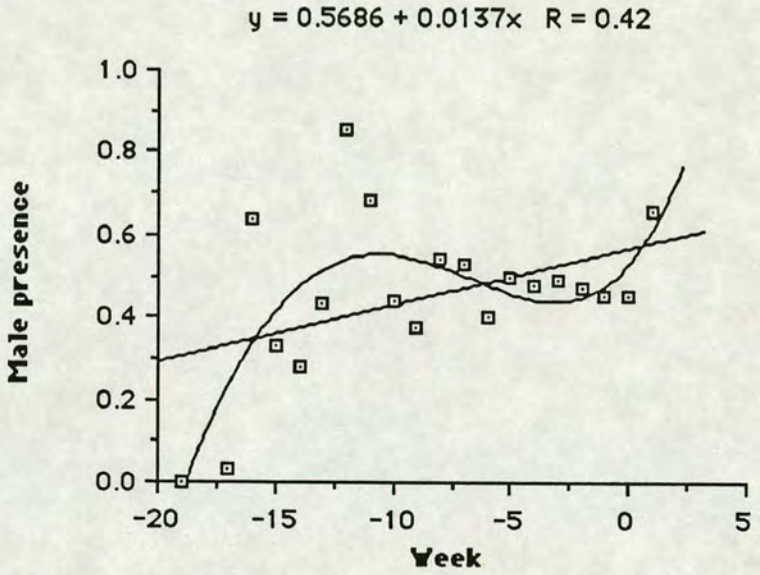
Interpretation of these results was difficult since nesting place presence was not independent of other activities besides roosting. Copulation and courtship feeding both required both birds to be present. Both behaviours had peaks in the morning (See Section 6.3.4, Figure 6.7, and Section 6.3.5, Figure 6.9), and might have affected the diurnal variation in nesting place attendance observed for Sparrowhawks.

6.3.2.2 Seasonal variation

The seasonal variation in Sparrowhawk presence at the nesting place by both

members of Sparrowhawk breeding pairs was determined from 1124.7 hours of observations from 125 days prior to the laying of the first egg to 11 days after. The relationship was plotted on a graph and a simple correlation and a third order 'best fit' line were calculated and drawn in. Statistical analysis was performed on the simple correlation. The polynomial description was used to suggest possible seasonal fluctuations in the rates.

Figure 6.4 Male Sparrowhawk presence at the nesting place (hours male observed at the nesting place/total observation bout hours) during the breeding season as a percentage of the time spent observing, 1986-1988. (0 = egg date; straight line = simple correlation, curved line = calculated polynomial 'best fit'.)

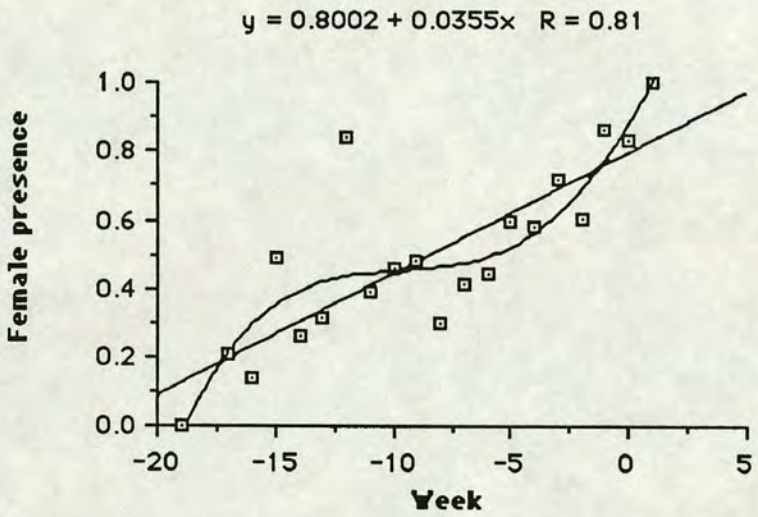


Male attendance did not increase significantly from the start of observations to egg laying. The source of much of the overall increase seen in the graph of male nesting place attendance is the low attendance rates early in the season (19 and 17 weeks before egg laying)(Figure 6.4). If the data from these two weeks are excluded, the lack of increase in male attendance is more apparent. The amount of time the male spent at the nesting place was significantly less variable for the 7 weeks just before the laying of the first egg than during the weeks earlier in the spring (F-test, df_1 = 9, df_2 = 9; $P < 0.01$).

In the one case where a yearling male replaced an adult as a breeder, the attendance at the nesting place by the two was similar. In the 7 weeks prior to egg laying the yearling spent an average (± S.E.) of 44 ± 4.9% of its time on the nesting place.

The population of long established males spent 47 ± 1.5% during those weeks. For the yearling the rate of attendance actually decreased in that 7 weeks, but the decrease was not significant. The attendance of a widowed male was unchanged (47 ± 1.3%) after the replacement of his mate. In the interval between loosing his original mate, and gaining a replacement, the male spent 53% of his time on the nesting place. This percentage was from only one 90 min observation bout in the late morning, so may have been biased.

Figure 6.5 Female Sparrowhawk presence at the nesting place (hours female observed at the nesting place/ total observation bout hours) during the breeding season as a percentage of the time spent observing, 1986-1988. (0= egg date; straight line = simple correlation, curved line = calculated polynomial 'best fit').



Female attendance increased significantly over the season (Spearman Rank Correlation (2-tailed, N = 20); $P < 0.02$) (Figure 6.5). Excluding the days when the female was incubating, and comparing week by week rates of increase in female presence, no significant change in the week-by-week rate of increase was seen.

A female which had lost her mate was more often seen at adjacent nesting places after the loss. In mid-April at nesting places adjacent to a place where a female had been widowed, the widow was seen to intrude on an adjacent nesting place 4 times in the week prior to loosing her mate (N=32 hours of observation). In the week after being widowed, that same female was seen to intrude on adjacent nesting places 11 times in 37.5 hours of observation. Some of these intrusions might have been a product of the female having to provide for herself, but some involved behaviours

associated with courtship (See sections on display and extra-pair copulation). Whether a widowed female was less attendant at the nesting place after losing her mate could not be proved. Replacement females did not differ from long established breeding females in their attendance rates; both spending an average of about 68% of their time at their nesting places during the 4 weeks before laying.

Female presence at the nesting place showed similar seasonal variation to the rate of food presentations, but whether this was coincidental or correlated was unknown. Throughout the day however, no correlation was found between the rates of female attendance and food presentations.

Simultaneous attendance at the nesting place by both members of a pair significantly increased over the season (Spearman Rank Correlation (2-tailed, N =20); $P < 0.02$) (Figure 6.6 and Table 6.4). Also, seasonal male attendance was significantly correlated to seasonal female attendance at the nesting place (Product-Mean Correlation Coefficient, $P < 0.05$). Peaks in both male and female attendance at the nesting place existed at 12 weeks prior to egg laying (See Figures 6.3, 6.5), but these were not very obvious.

When at the nesting place together, males and females were not necessarily very close to one another. Although no detailed information was collected, pair members were close (< 3m apart) mostly after either feeding, or copulation, or at the nest during building activities, at other times they kept their distances.

Throughout the season, the variation in concurrent nesting place attendance through the day was confused by the female starting to roost on the nesting place after pair establishment, and the necessity of the male to be away from the nesting place while hunting while at the same time, the female's hunting duties were decreasing. Other factors such as age of breeders, weather, and prey availability could have affected attendance. However, their affect was not analysed.

In the two weeks prior to egg-laying, at 6 nesting places where the egg-dates and ages of the breeders were similar, no significant difference in the amount of time spent together at different times of the day was seen. A small peak in concurrent nesting place attendances occurred around 0900 hours, when the male would have returned from hunting, and the female would have just fed. See Section 6.3.4 for the effect of feeding on nest site presence.

Figure 6.6 Concurrent presence of both members of breeding Sparrowhawk pairs at the nesting place (as a percentage of total observation time) during the breeding season as a percentage of the time spent observing, 1986-1988 (straight line = simple correlation, curved line = 'best fit').

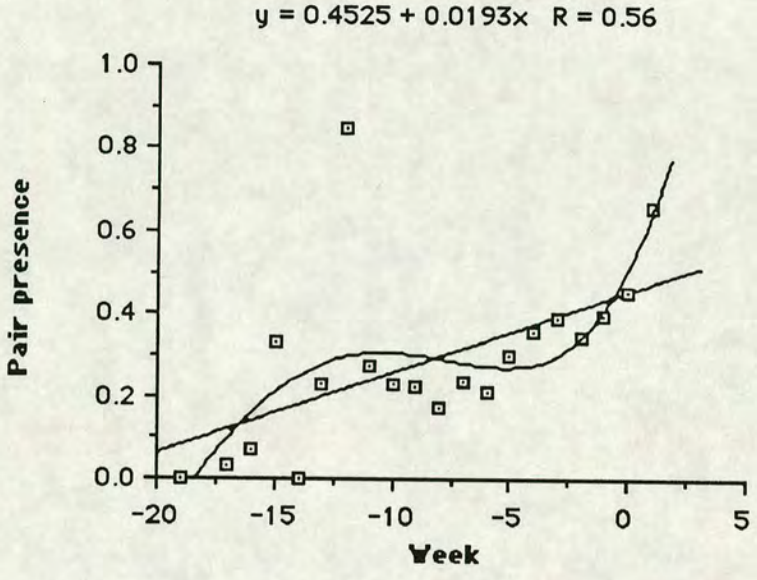


Table 6.4 Mean percentage (± S.E.)of time male and female were in attendence at the nesting place as individuals and as a pair in Edinburgh 1986-1989.

	No. of days before first egg			
	30 days	**20 days**	**10 days**	**5 days**
Male N=8	52.2±4.2	43.3±3.8	49.8±4.7	50.9±5.1
Female N=10	52.1±6.0	71.1±4.1	75.5±2.1	89.8±0.7
Male and Female N=6	37.1±4.1	39.9±4.1	41.9±3.9	47.0±4.6

Means were drawn only from birds or pairs whose attendance history was known throughout the 30 day prior to laying eggs

6.3.3 Display

Display behaviour was observed in yearlings and adults of both sexes. It was seen in both mated birds and in individuals which had no mate (either because of an inability to attract one, or due to the loss of an established partner). Replacement of breeders

was quick; no difference in the types or rates of displays could be seen in widowed individuals. Display behaviour ranged from simple calls to complex assemblages of flying, posturing, and calling. Some displays were performed individually, but at times aerial displays involved up to 7 individuals of both sexes, some of them paired.

Variations of both defensive and courtship calls and displays are numerous and have been described previously (Jones 1974; Newton 1986; Owen 1916; and Cramp and Simmons 1980). Similar displays are used for both defense and courtship purposes, making it difficult to assign a function to many of the displays observed. To determine whether a display behaviour was defensive in nature or related to courtship the context in which it occurred was examined. The presence of an intruder, the sex of any intruder, what types of calls were associated with the aerial display, and the temporal proximity to other defensive (i.e. chasing an intruder) or breeding behaviours (i.e. copulation) were used in the determination. If there was any confusion, the display was excluded from this analysis.

Although I may have assigned a purpose to a particular display, this did not necessarily coincide with the result of that same display. Some displays classed as 'courtship' may have also functioned to inform possible intruders of the occupied status of a nesting place; conversely, 'defensive' displays may have served to cement the pair-bond or attract a mate. Since more defensive displays occurred at the nesting place, and ended without the individual going out of sight, relatively more information on the specifics of these displays was collected.

Aerial displays (for unknown purposes) occurred in the autumn and winter. Both courtship and defensive displays occurred throughout the breeding season. I did not examine the seasonal variation in the rate of either courtship or defensive displays since the time between establishment of breeders on the nesting place was so variable, and since defensive displays were dependent on intrusion rates (See Section 6.3.3.2). Still, more displays (N=402) of all types were seen as egg date approached (χ^2 (two-tailed)= 261.2; N = 7 week-long periods, df=6, $P < 0.01$). This must be at least partly because more birds were established as pairs later in the spring.

The percentage of all displays which were for courtship, rather than defensive, purposes was higher, but not significantly so, early (>4 weeks prior to mean egg date) in the spring (See next section). However, this result may have been

influenced by my inability to assign a motivation to all of the displays witnessed.

Weather affected the display behaviour of both breeding and non-breeding male Sparrowhawks. Examining the display behaviour of a non-breeding male, and a breeding male, both of which were radio-marked from 1-15 April. Both birds were seen to soar more often (31 soaring bouts) on warm clear days than on cold, rainy ones (χ^2 (two-tailed) = 45.8; $P < 0.05$). The mean amount of time spent by these two birds during these soaring bouts was not significantly different, but was influenced by relatively few instances of rainy-day soaring. A greater sample size of days for more individuals is needed to make any pronouncement. The seasonal change in the rates of other activities (such as hunting, and nest-building) of both breeders and non-breeders must also have affected display rates.

6.3.3.1 Courtship display

Displays which functioned as a means of advertisement, pair-formation, or pair maintenance were all classified as 'courtship' displays. Four types of display were obviously associated with courtship: soaring, slow-flighting, undulating and perch and call. A display combining all of these displays was also observed. Still, these displays which functioned primarily in courtship may also have had a secondary, defensive purpose. Courtship displays were witnessed as early as mid-December and continued until just prior to the laying of the first egg.

Combined displays performed by both members of the pair, in the absence of any intruder seemed most closely linked with courtship. They were least likely to be confused with displays for other purposes. This is not to say that these displays did not also have some defensive component. Both adults and yearlings were seen to participate. Adjusting for the number of morning and afternoon observation hours, 89% of combined displays occurred in the morning. In most cases, it was difficult to determine which member of the pair initiated the display. When performed by un-established birds with a breeder of the opposite sex, the display often did not finish at the nesting place. In these instances it was not possible to determine whether the display was initiate by resident or intruder.

'Typical' courtship displays sometimes followed an intrusion event. In 11 out of 17 cases in which an intrusion occurred while both members of the pair were at the nesting place, a courtship display by the paired birds followed within 10 minutes of

the intrusion. I could not always be certain that intruders had in fact been driven off completely prior to the initiation of the courtship-type display.

Widowed birds of both sexes were seen to perform courtship displays. At times the un-established bird which became the replacement partner participated in these displays. As the new pair was formed the number of courtship displays performed exclusively with the replacement bird increased.

6.3.3.2 Defensive displays and intrusions

It was sometimes not possible to determine whether a display was defensive, since these displays may have been directed against an intruder I did not see, or against potential rather than actual intruders. Not all intruders were immediately detected by the territory holder(s). This was different from 'tolerating' an intruder, and was usually characterized by a sudden, and often very aggressive, defense response once the intruder was noticed. Un-noticed intruders entered occupied territories at all times of the day and throughout the season. In particular, these occurred around mean egg-date, and in the evenings. The undetected intruder sometimes roosted at the occupied nesting place. Some analysis of these undetected intrusions is undertaken in Chapter 4.

The displays by established breeders which were most unambiguously defensive were those directed against intruders at the actual nesting place, at tree level. Sixty four percent (N = 212) of the defensive displays were in the morning. It may have been that the elevated defensiveness was due to a peak in the intrusions by non-pair individuals (both breeders and non-breeders) at that time (See below). Some of the attacks on intruders by territory holding Sparrowhawks occurred after the intruder had roosted at the nesting place of the defender. These interactions are discussed more fully in Chapter 4.

A total of 361 intrusions by non-pair individuals were observed. The rate of intrusions by non-pair Sparrowhawks of both sexes onto all nesting places under observation showed no sign of seasonal change. The number of intrusions at a particular nesting place was highly variable from day to day. The number of intrusions by different individuals in an hour of observation ranged from 0 to 4. Most (69%, corrected for number of observation hours) of intrusions were in the morning.

The number of intrusions by unmarked (and probably un-mated) birds at two nesting places in which all neighbouring breeders were colour and/or radio tagged increased, although not significantly, as mean egg-date approached (Spearman Rank correlation (1-tailed), N=18; P > 0.05). Early in the season (> 3 weeks prior to date of first egg) at these same two places, the number of intrusions by yearlings (24) was similar to those by adults (22) (the adults were usually colour-marked breeders from adjacent nests). Correcting for the difference in the number of morning and afternoon observation hours at the two nesting places, 74% of the intrusions were in the morning. In the week prior to egg laying 19 of 25 intruders were un-marked individuals, presumably non- or later breeders. Seventeen (68%) were yearlings.

Intruders of both sex were chased by territory holders of both sex (Table 6.4). There was an indication that defensive reactions were strongest against intruders of the same sex. In all situations where a single, but still paired Sparrowhawk was on a territory, an intruder of the same sex was attacked (N = 70). Table 6.5 summarizes the responses of the breeders to the intrusions.

Table 6.5 Proportion and sex of intruders attacked by territory holding Sparrowhawks in Edinburgh 1987-1989. This includes only cases when the territory was being attended by only one member of the pair.

	Sex of Intruder	
	Male	**Female**
Sex of Breeder		
Male	31:31	26:37
Female	43:48	39:39

In 4 cases at 3 nesting places when both members of the breeding pair were in attendance, intruders were tolerated, but only after a prolonged bout (>10 minutes) of defensive calls, displays and chases failed to drive them off. In all cases the intruder was a yearling and both breeders were adults. In all cases, the intruder was a female. I could not examine whether yearlings were allowed to intrude more closely than adults, although in all cases where replacement of a breeder occurred, the new

member of the pair was a yearling.

On 9 occasions intruding females solicited copulations from the male. Two solicitations occurred with the territory holding female in attendance. In those cases, it appeared that the intruder had not been noticed since the intruder was attacked by the resident female immediately after soliciting. On 5 occasions extra-pair copulations occurred (See Section 6.3.5).

Age of female intruder seemed not to be important in determining the defensive response of the male, as both yearlings and adults were treated similarly. Also, yearling (18) and adult (20) males were tolerated, and defended against, by breeding females of both age classes. The age of male intruders was not always determined. No extra-pair copulations were witnessed with an intruding male.

A non-breeding yearling female that entered an unattended nesting place was seen to attack the resident (adult) female when she returned. Eventually the yearling was driven off. I do not know if she went on to breed.

Birds of both sexes which had recently (within a few days) lost their mate and had not yet found a replacement were seen chasing intruders of both sexes and age groups from their nesting place. In two cases where a member of the pair had been killed and a replacement had not been found, the widowed bird was seen to tolerate intruders of the opposite sex 87% of the time (N=16), and members of the same sex 50% of the time (N=26). These percentages were not significantly different at the 95% confidence limit, and did not differ significantly from the defense rates of paired birds which were in single attendance at the nesting place (See above). Widowed birds were also seen to intrude on neighbouring nesting places in the time between the loss of one mate, and pairing with another.

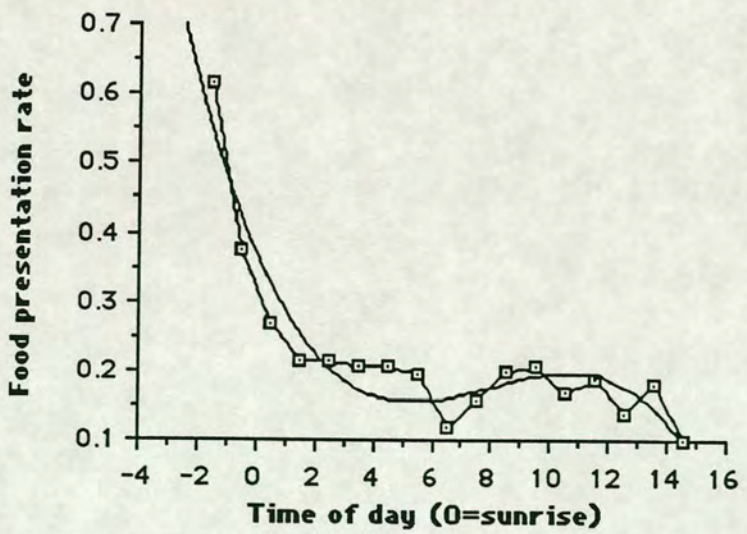
It was unknown whether intrusions were the result of individuals prospecting for vacancies in the breeding population, attempts to oust the resident, a means of seeking extra-pair copulations, or just a consequence of the ranging (foraging) behaviour of the individual. The behaviour of radio-marked birds examined in Chapter 4 suggests a possibility of prospecting for breeding opportunities. Aggressive displays by an intruder toward a resident bird of the same sex were seen. In only one case was there an intimation that these aggressive displays may have resulted in a resident being driven off and replaced, but this could not be proven.

6.3.4 Food presentations/courtship feeding

Vocalizations and overall behaviour of Sparrowhawks during courtship feeding are described by Newton (1986). In Edinburgh, presentations of food by the male to the female were observed at all times of day, between 0510 hrs and 2023 hrs. Away from the nesting places, male Sparrowhawks were seen to be carrying plucked prey in May as early as 0350 (very low light), so it is possible that some prey deliveries were missed in the very early mornings. The relationship between food presentation rates and time (of day and in the season) is graphically represented. A third order polynomial, 'best-fit' line has been calculated and drawn, to suggest fluctuations in food presentation rates.

Hourly food presentation rates were calculated from 799 full hours of observation. Figure 6.7 illustrates the distribution of food presentations throughout the day. The morning rates were not significantly higher than those in the afternoon (Spearman Rank Correlation (2-tailed, N = 16) (Figure 6.7). A mean of 0.23 $\pm$ .02 food presentations/hour were made. Food presentations 1-2 hours before sunrise were more frequent than at any other time of day (Dixon's test for outliers (N = 16); $P < 0.01$).

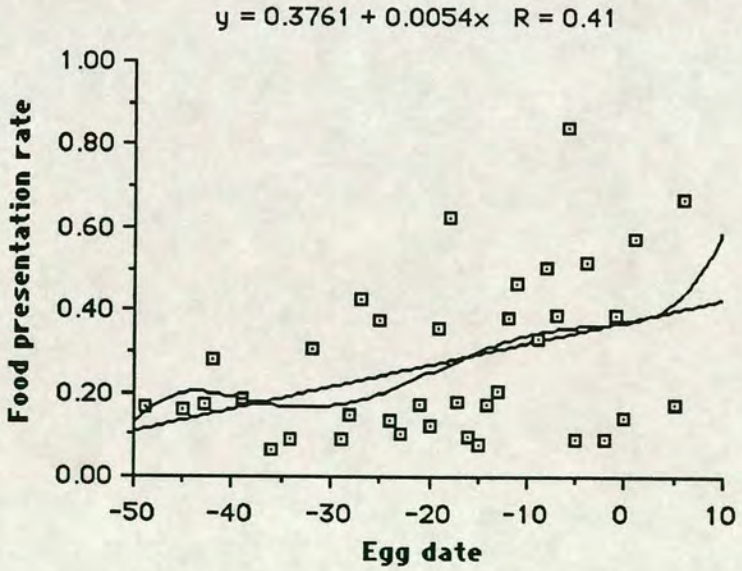
Figure 6.7 Diurnal variation in the rate of food presentation (per hour) by male Sparrowhawks during the breeding season in Edinburgh, 1986-1988 (Curved line = calculated, polynomial 'best fit').



Courtship feeding started at different times for different pairs. Some males would start presenting food to their mate as early as February. Some females hunted until just a few days before egg-laying, their diets being supplemented by the prey presented by their mates. Others seemed wholly dependent on the cock for food for up to 7 weeks before egg-laying, but I could not be certain that they were not doing some hunting as well.

Seasonal variation in food presentation rates was examined, and plotted from 849 hours of observation. These rates were calculated only from observations made on pairs where the male was believed to be the exclusive provider of food. Observations of courtship feeding were made from 49 days prior to the laying of the first egg to 11 days after. In plotting the rates, I excluded days in which no food presentation were observed. Rates of food presentation ranged from 0.066 to 0.842 presentations/hour. These rates were calculated for 36 and 6 days prior to egg date respectively. Rates of food presentation increased significantly as egg date approached (Spearman Rank Correlation (2-tailed, N = 37);P < 0.05). These data gave a mean of 0.277 food deliveries/hour (Figure 6.8).

Figure 6.8 Seasonal variation in the rates (per hour) of food presentations by male Sparrowhawks during the breeding season in Edinburgh, 1986-1988 (straight line = simple correlation, curved line = calculated, polynomial 'best fit').



Calculating from the two mean values of hourly food presentation, and an estimate of the number of daylight hours available to male Sparrowhawks (650) which are

providing entirely for the females, between 148 and 180 food deliveries are made to the female prior to laying the first egg. The number of presentations by a particular male was in part dependent upon when he initiated courtship feeding, and how early he became sole provider for the female.

Seasonal variation in rates of female attendance at the nest and food delivery rates were not significantly correlated. Male presence could not be correlated to food provisioning since hunting and time spent at the nesting place were not independent of one another.

Not all food presented to the female was eaten immediately. Some prey items were cached in the fork of a tree or on a limb, and not always retrieved. If an intruder came to the nesting place when food was being delivered, the item was often dropped, and not retrieved.

In 16 cases the female did not accept food offered to her by the male. He would then fly through the trees calling, perch on an obvious branch, and exaggeratedly pluck at the prey item. If the female still did not take the prey the male would either cache or drop it. No observations were made of males eating an entire prey item which had been refused by a female (See section on copulation for analysis of the relationship between feeding and copulation.).

In one instance an intruding yearling female received food from a breeding adult male. The resident adult female was not present. This occurred 37 days before egg laying. The intruder was not known to breed in that year.

6.3.5 Copulation

Newton (1986) described the 'typical' copulatory behaviour of Sparrowhawks. In Edinburgh, variations on this basic behaviour were also observed. In some instances no solicitation by the female was seen prior to a successful copulation. How the female communicated to the male that she was willing to copulate was unknown.

During a copulation attempt the male might call very softly. Calls were also occasionally heard both immediately before and after some copulation events. The calls prior to copulation attempts were usually made by the female when soliciting. Newton (1986) describes this call. Both males and females would sometimes call

after copulation. These were similar to defense calls, and in some instances may have been in response to other Sparrowhawks which were seen flying nearby.

Not all copulation attempts were successful. In some instances the male mounted the female, but no cloacal contact occurred. The success of all copulation attempts could not be confirmed, but at least 5% of all attempts between members of the same pair were unsuccessful. The mean duration of a copulation attempt was 9 seconds (Range = 3-13).

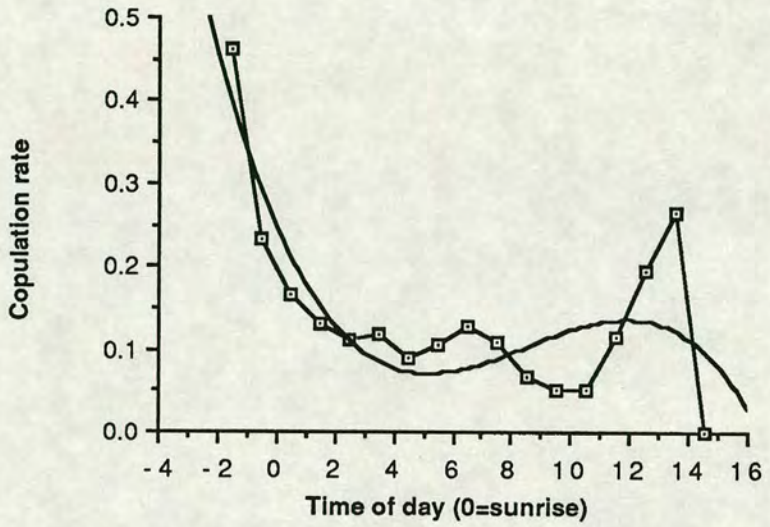
Copulation rates were calculated for each hour of the day (relative to sunrise) using 835 full hours of observations of established pairs (Figure 6.9). These observations were made between 51 days prior to egg laying and 8 days after and included only successful copulations. Copulations occurred as early as 0352 hrs and as late as 2031 hrs. A mean of 0.18 $\pm$ 0.04 copulations were attempted per hour. The copulation rate 1-2 hours before sunrise was significantly higher than at other times of the day (Dixon's test for outliers; $r_{22} = 0.557$, $P < 0.05$).

Seasonal variations in copulation rates were calculated from 139 copulation attempts witnessed during 860 hours of observation between 51 days before and 8 days after the laying of the first egg. Copulations did occur earlier, but these were either witnessed outside formal behavioural observation times, or were between individuals which did not remain as a pair. Extra-pair copulations also occurred, and are discussed in Section 6.3.6.

Throughout the season (-51 to +8 days), Sparrowhawks attempted to copulate a mean of 0.13 times/hour. A 'maximum' rate, of 0.22 $\pm$ 0.02 (S.E.) copulations/hour was calculated by including only those days in which copulations were observed. These rates varied between pairs, between days, and between years; in 1987 the copulation rate observed was twice that of the other two years (Table 6.5). This difference though was not significant (χ^2). There was no seasonal increase in copulation rates as egg date approached. Copulation was observed after egg-laying, but in only one instance was copulation observed after incubation had started.

Excluding the days after the first egg was laid, when the female may have been less available to the male due to her being more attentive to the nest and egg(s), and looking at the data in a step-wise manner from 51, 21, 14, and 7 days prior to the laying of the first egg, no significant increase in copulation rate occurred.

Figure 6.9 Diurnal variation in copulation rates (per hour) of Sparrowhawks in Edinburgh, 1986-1988, based on observations made between 51 days before egg laying and 8 days after. (Curved line = calculated, polynomial 'best fit').



Between 1 February and 10 May there are about 1200 daylight hours (sunrise-sunset). Given these rates, a conservative estimate of 149-264 copulatory attempts are made by a pair of Sparrowhawks which established itself early and remained together until at least the egg date.

Provisioning of the female by the male seemed related to copulation in that their daily variation was similar, with a peak in the morning, and perhaps a lesser one in the afternoon (Figure 6.10). This relationship might be partially explained by the fact that these activities were not always independent; both requiring that both pair members were present. Through the season, the variation in provisioning rates was also similar to the variation in copulation rates (See Section 6.3.4, Figure 6.10, and Table 6.7). In as much as copulation was coincidental with food presentations, and food presentations were made after the male had been hunting (and was therefore absent from the nesting place), copulations were related to male absence.

Table 6.6 Summary of the seasonal copulation rates of Sparrowhawks in Edinburgh, 1986-1988.

Yearly

	1986	1987	1988
Copulations	29	57	33
Rate (Copulations/hr*)	0.15	0.28	0.13

Overall (Copulations/hour)

including all days (-51 to +8)	0.16
only days when copulation was observed*	0.22
including all days (-125 to +11)	0.124

*'Maximum' rate calculated excluding days between -51 and +8 when rate =0.

In some pairs, at around 50 days prior to the egg-date, the initiation of exclusive feeding by the male was coincidental with the onset of regular copulations. Many copulations occurred soon (within 5 min.) after the presentation of food, but many also occurred over an hour later. The distribution of post-feeding copulation fit a negative binomial distribution (Kolmogorov-Smirnov test for intrinsic hypotheses; $N = 12$, $D = 0.04$, $p < 0.05$) (Figure 6.11), showing no clear link between food presentation and copulation.

Figure 6.10 Comparison between the daily variation in copulation and food presentation rates (per hour) of Sparrowhawks in Edinburgh, 1986-1988.

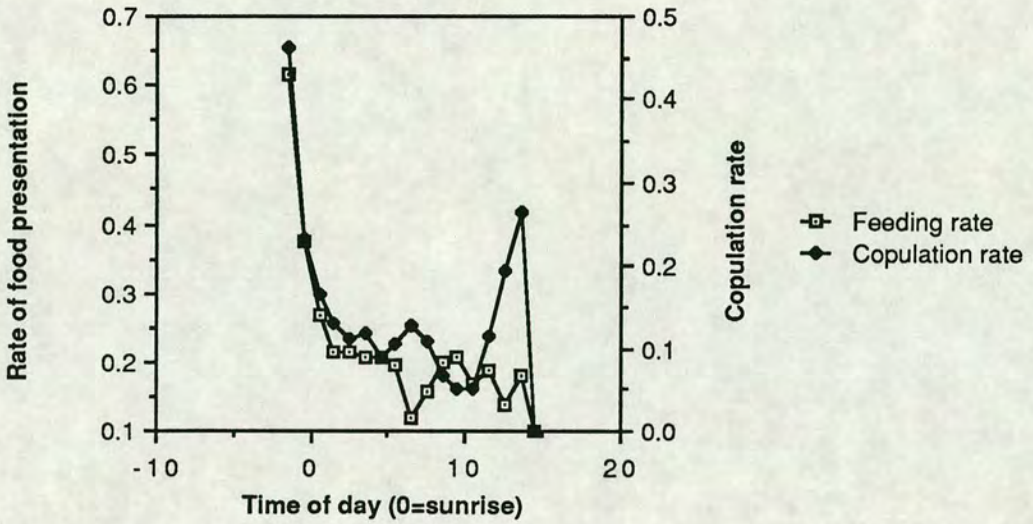


Table 6.7 Mean weekly copulation and food presentation rates *(events/hour ± S.E.) of Sparrowhawks for the 5 weeks prior to egg laying in Edinburgh in the years 1986-1989.

	Week before laying				
	1	**2**	**3**	**4**	**5**
Copulation rate	.33±.05	.209±.032	.251±.053	.243±.052	.139±.051
Food presentation rate	.519±.081	.404±.06	.389±.061	.201±.049	.193±.054

* rates tabulated do not include the copulation and food presenation rates in pairs which were not maintained for all of the 5 weeks prior to egg laying.

6.3.6 Extra-pair copulations (EPC's)

Twenty-one extra-pair copulations (EPC) were observed. This was 13% of the total number of all copulations. All were observed on the territory of the participant male. In 4 cases an intruding female solicited but got no reaction from the resident male. In 5, copulation occurred after female solicitation. For the other 17, solicitation was not witnessed.

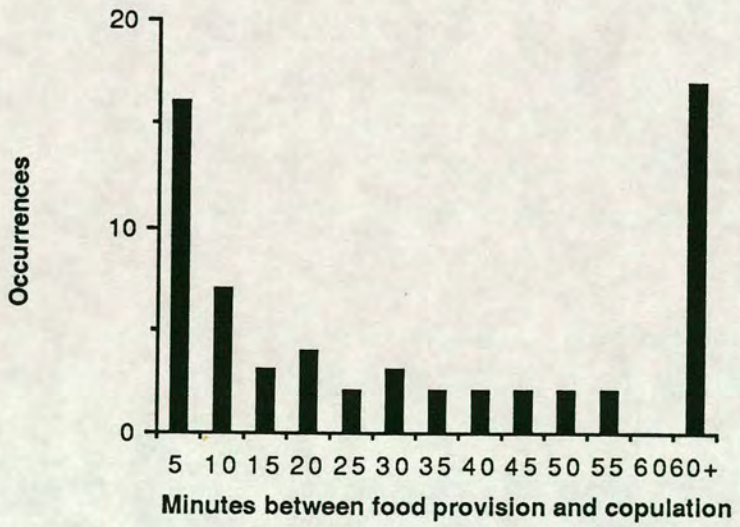
In 9 cases the extra-pair copulation occurred between an established male and a female that was known to be paired with a different male. Males were always adults.

Females were were both adult and yearling, and were, in 10 instances, residents of adjacent nesting places. In 1 case the female was resident further afield. In the others, the female could not be identified (And was not known to be paired), although it may have been from a nearby nest. Two copulations were witnessed between a widowed female from an adjacent territory and a paired male.

EPC's occurred mainly in the morning (between 0714 hrs and 1238 hrs; only one occurred in the afternoon), between 18 March and 1 May. In situations where the identity of the female was known and she went on to produce eggs in that year (N=12), EPC's occurred between 32 days and 9 days prior to the laying of the first egg. Ten (83%) were between 21 and 9 days before the first egg.

DNA fingerprinting confirmed that EPC's might lead to extra-pair fertilizations (Chapter 5), although the presence of sperm storage tubules in the female reproductive tract (Section 6.3.7) could allow for fertilization by any male that copulated with the female.

Figure 6.11 Amount of time between food presentation by the male and copulation in Sparrowhawks in Edinburgh, 1986-1988.



6.3.7 Sperm storage

Sperm storage tubules were located in the reproductive tract of both female Sparrowhawks examined. These were sometimes difficult to distinguish from the surrounding tissue and at times it was the presence of sperm within them that indicated their presence. There were almost no sperm in the tubules of the bird caught in the late afternoon. The results of transects of the area of highest tubule concentration in the females caught in the morning are presented in Table 6.6

The actual structure of the tubules could not be determined, but they were three dimensional in nature (Plate 6.1 (a) and (b)). The greatest concentration of tubules were seen about 13 mm distal to the entrance to the uterus in the stretched and dissected vagina.

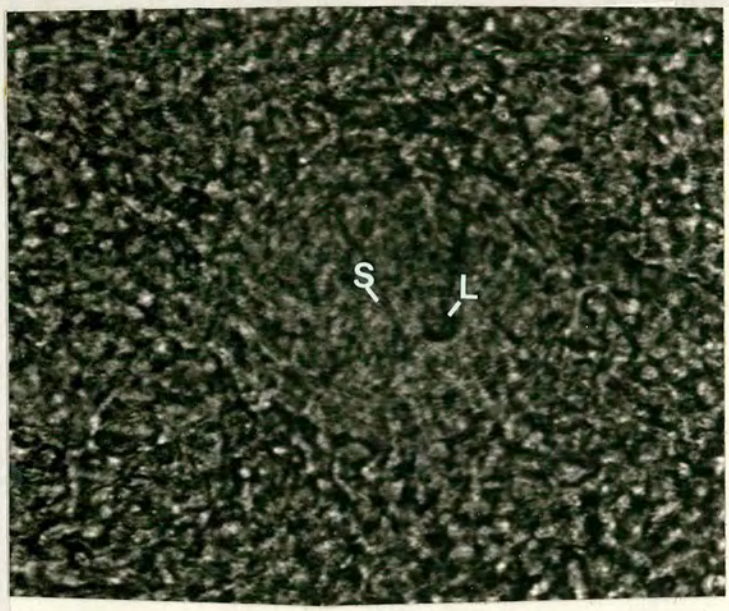
The mean number of sperm per tubule was 4.25. The maximum number was 33. There was no obvious relation between the position of the tubule within the reproductive tract and the number of sperm which were stored. The length of time which a sperm could remain viable while stored was not known, although those observed seemed normal.

Table 6.8 Counts of sperm storage tubules and the sperm stored within them on four transects of the reproductive tract of a breeding yearling Sparrowhawk.

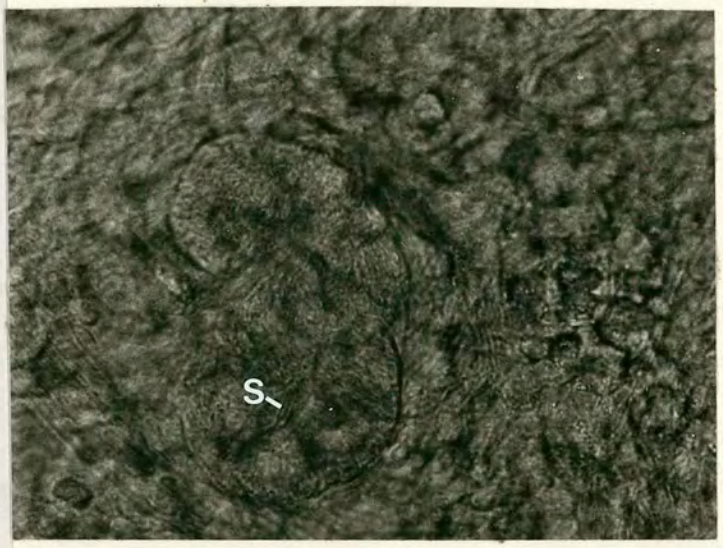
No. of Sperm	No. of Tubules	No. of Tubules w/ no Sperm
10	12	7
161	39	8
304	58	8
265	39	8

Plate 6.1(a) and **(b)** Sparrowhawk sperm storage tubules. L = lumen, S = tails of stored sperm.

(a)



(b)



6.4 Discussion

Since Sparrowhawks have a relatively low annual survival, and have at most, one opportunity to raise a brood per year, it is important to utilize every chance to breed, and breed successfully (Newton 1989). The fact that neither the male or

female can raise a brood without the help of their mate means that a mixed monogamous reproductive strategy is the most efficient way for individual Sparrowhawks to maximize reproductive success (See: Trivers 1972; Fitch and Shugart 1984). In many animals including Sparrowhawks, the reproductive strategies employed by males and females are sometimes in conflict. Parker *et al.* (1972) argue that this conflict in the form of gamete competition, and later sperm competition may have accounted for the origin of the two sexes in multicellular organisms.

The establishment and maintenance of the pair-bond is of prime importance to Sparrowhawk reproductive success (Newton 1986). To achieve maximum lifetime reproductive output, it is best for individuals to pair with high quality, adult mates on good quality territories early in the nesting season (Newton 1986), and to breed every year from the first year of life (Newton 1989).

In Sparrowhawks, the male's reproductive success is primarily tied to his success in finding mates rather than the production of gametes (See: Trivers 1972). So, a male that pairs with a female of high quality, but is open to EPC's with other females is at an advantage. In this reproductive strategy, the bulk of the male's effort is at his nesting place, and any offspring produced through EPC's are a bonus. If males engage in EPC's, it is advantageous for each individual to avoid being cuckolded. Two aspects of reproduction, one behavioural and one physiological can enhance paternity: mate guarding (Birkhead 1979) and sperm competition (See: Smith 1984). The established female's reproductive success is tied to pairing with a male of high quality, especially since she is completely dependent upon him for food during part of the breeding season. She should however be open to EPC's as a hedge against male infertility, or as a means of being fertilized by a male of higher quality than the one with which she is paired.

Unpaired Sparrowhawks should pursue a strategy that enhances their prospects of becoming a successful breeder by associating with all possible mates (Trivers 1972). For the male non-breeder it is best to become an established breeder, but it would also be advantageous to be a cuckold. As a cuckold of another territory holding male, he may increase his annual reproductive success without incurring the associated cost of nestling care. Females which are non-breeders, but would breed if an opening occurred in the breeding population, should be prepared to copulate with all males (particularly established ones), and thereby enhance the likelihood of their raising a brood. Some non-breeders are not in a physical condition to pursue or

attract any mating opportunities.

The breeding behaviours of Sparrowhawks in Edinburgh reflect the reproductive strategies of the male and female. Broadly, the descriptions of the breeding behaviours of Sparrowhawks presented by other researchers (Newton 1986; Owen 1916-1937; Cramp and Simmons 1980; Brown 1976; Brown and Amadon 1968) are consistent with the more detailed examination of those same behaviours presented here. Any variation in the behaviours themselves is probably due to variations in individual birds, or in the particular breeding situation.

All behaviours by breeding Sparrowhawks during the spring are probably inter-related. Nesting place attendance by the members of the pair, the level of defensive-ness, feeding rates, and within-pair- and extra-pair copulations (WPC's and EPC's) are particularly difficult to dissociate from one another. Behaviours are also inseparable from the environment in which they occur (McKinney *et al.* 1984).

In raptors in general, the guarding of the female by the male can never be 100% efficient, since at times the male provides her with food during her fertile period and is therefore away from both mate and nesting place during hunting. The evidence that male Sparrowhawks did attempt to guard the female is equivocal. The significant correlation between male and female seasonal attendance rates at the nest was high-lighted by the peaks seen early in the breeding season. These simultaneous peaks may argue against the attendance rates of male and female Sparrowhawks being merely coincidental. However, if the mornings are the time when females are most fertile (See later, and Lodge *et al.* 1971), we would predict that males would be near the females more at this time. This was not the case for Sparrowhawks in Edinburgh. The diurnal variation in both male and female attendance rates, with peaks in the morning and the evening, might only have been a consequence of them roosting at the nesting place, rather than a result of an actual effort to attend to a mate.

Since guarding cannot be complete, the female (and male) are available for EPC's. With the male's ability to guard the female compromised, other means of ensuring paternity must be employed in addition to guarding. For the male, other possible means of enhancing chances of paternity include forced copulations (Cheng *et al.* 1983), high copulation rates, and engaging heavily in copulations during the female's most fertile period.

Forcing the female to mate presumably serves to ensure that a male's sperm is the freshest within the female and perhaps therefore the most likely to fertilize the egg. Forced copulations are presumably not possible in Sparrowhawks since the female is sometimes twice as large as the male. Even in species where forced copulations occur, their effectiveness as a means of ensuring paternity has been questioned (McKinney *et al.* 1984).

Another means of enhancing the probability of paternity is a high copulation rate (Martin *et al.* 1974; Birkhead *et al.* 1987). High copulation rates have been reported in other raptors (Willoughby and Cade 1964; Balgooyen 1976; Village 1990). Established Sparrowhawks copulated frequently, their copulation rate being in line with those of other diurnal birds of prey which nest singly (Birkhead *et al.* 1987), but less than that reported in the Goshawk (Møller 1987). In particular, the higher number of copulations/clutch in the Goshawk was a result of a higher number of copulations/hour since the pairing of male and female Goshawk did not commence as early as was observed in the Sparrowhawk. Observations of breeding Sparrowhawks did not extend far beyond the fertile period, so no comparison could be made with the behaviours of Goshawks in the post-fertile period. In Goshawks, after eggs were laid, the copulation rates declined markedly (Møller 1987).

Copulation rates may vary in connection with population size and composition, habitat type, and size of home range. One might expect copulation rates to be high in populations in which there is an excess of one of the sexes, and/or if there are more potential breeders than there are nesting places to accommodate them. The number of copulations per year and the rate of copulations per hour in the Sparrowhawk in Edinburgh do not seem inconsistent with the expectations. In Osprey, first time breeders were unsuccessful in copulation attempts more often than experienced birds (Birkhead and Lessells 1988). This could not be examined by this study.

Whether the male or the female claim the territory initially is equivocal (Newton 1979), but in Sparrowhawk is probably the male (Newton 1986). The importance of copulation in the establishment and maintenance of the pair-bond could not be easily assessed, but should not be discounted. As in Goshawk, Sparrowhawk copulation rates showed a peak early in the season, when the chance of insemination was probably lower than the time just prior to egg laying (Sturkie 1976; Lake 1975; Lodge *et al.* 1971). Møller (1987) suggested the early peak in copulations in Goshawks was caused by an increase in copulations as a means of pair formation.

There were too few observations of copulations at that time to be sure of the relationship between copulations and pair formation, however, a relationship between nesting place attendance and pair formation is suggested in Sparrowhawk.

Sperm storage tubules (SST's) were found in the reproductive tract of the female Sparrowhawk, and are known to exist in other raptors (e.g. American Kestrel: Bakst and Bird 1987) It is unknown whether in the Sparrowhawk SST's facilitate the production of fertile eggs from copulations early in the year. In other groups of birds the length of sperm storage and fertility can be very long (e.g. Turkeys: 40-50 days, Lake 1975). Goshawk were fertile for at least 4 days prior to egg laying (Berry 1972), and American Kestrel *(Falco sparverius)* up to 12 days (Bird and Buckland 1976). In other raptors, fertile eggs were laid 9 (Golden Eagle, Grier 1973) and 10 days (Peregrine Falcon, Fessner 1970) after insemination.

Although the male is unable to physically force the female to copulate, it would be to his advantage to be able to manipulate copulations by other means (Safina 1984). The interdependence of the breeding behaviours studied, and the similarity of their distribution throughout the day and throughout the season made it difficult to separate cause and effect.

In Sparrowhawks, copulations were more likely to happen after the male had been away from the female and the nesting place. It was not known whether these copulations were caused by, or were coincidental to his absence. In Goshawk, Møller (1987) suggested that the copulation rates may be related to the time spent away from the nesting place by the male. He compared the mean time spent away per day by the males of three raptor species including the Sparrowhawk. His analysis is based on an assessment that the copulation rate in Sparrowhawks is low. This is not a characteristic of the Edinburgh population. In Osprey conflicting findings on whether the amount of time that a male was absent affected copulation rates have been reported (Birkhead and Lessells 1988; Green 1976). If copulation rate were related to male absence, would a female that is paired to a low quality male, one which had to spend more of his time hunting, copulate more often with him? Certainly, the relationship between copulation rates and male absence is not clear. Copulation rate increases in Sparrowhawks were at least coincidental with the increase in the amount of time spent at the nesting place by the female, the male, and the pair together.

The connection between food and reproductive success has been made: well-fed female Sparrowhawks are more productive (Newton and Marquiss 1981). Increased female weight might be a result of increased prey presentations in the spring for purposes of buying copulations, making the female less likely to leave the nesting place, and/or to enhance egg production and incubation.

There was no evidence that males bought copulations with food. Many copulations occurred soon after food presentations, but some occurred much later. Although the distribution of times between food presentation and copulation was non random, the lack of independence between food deliveries and male absence clouded the issue. Still, in Sparrowhawks as laying date approached, both the rate of food presentation and the rate of copulations increased. In Goshawk this correlation was significant (Møller 1987), but in Osprey there was no evidence that food was traded for copulations (Birkhead and Lessells 1988).

The relationship between presentation of food and mate guarding by the male was unproven. As expected, a fed female was more likely to stay at the nesting place, and was likely to perform other breeding behaviours, such as nest building, and courtship and defense display. In Osprey, Green (1976) reports that courtship feeding is related to the amount of time the male remains at the nesting place, but Birkhead and Lessells (1988), working on the same species found no such relationship. Møller (1988) notes that males and females of Honey Buzzard *(Pernis apivorus)* and Hobby *(Falco subuteo)* hunt together, allowing for more effective guarding by the male. It might have been that any possible correlation between food presentations, and attendance by the females was hidden by the tendency of females to loaf at the nesting place in the afternoon when food presentation rates (and the rates of most other behaviours) were low.

To maximize the chances of fertilizing his mate, males may attempt to mate with the female when she is most fertile. In general, the closer to ovulation a copulation event occurs, the more likely that particular sperm will inseminate the egg (Lodge *et al.* 1971). In Sparrowhawks there is no significant increase in the copulation rate as the egg-date approaches. In Goshawk there is a peak in copulations between day -22 and -5 (Møller 1987). During the pre-lay period, no increase in copulation rate was seen in Osprey (Birkhead and Lessells 1988).

The phenology of egg fertilization in Sparrowhawks is not well known, but is impor-

tant when examining the copulation rates in relation to diurnal cycles of female fertility. In domesticated birds which also lay multi-egg clutches, the time needed for the spermatazoa to fertilize the ovum can be as short as 15 minutes after ovulation (Sturkie 1976). In chickens, Lodge *et al.* (1971) found that egg hatchability was highest in zygotes formed from sperm which had been in the female reproductive tract about 48 hours. In American Kestrels, at most 24 hours was needed for fertilization to occur, and 24-36 hours for egg formation (Bird and Buckland 1976).

Since most Sparrowhawk eggs are laid in the morning, the morning peak in copulation rates may be related to ovulation, and therefore a peak in female fertility. This is the explanation given for a similar peak in the Goshawk (Møller 1987), as well as an afternoon peak which is not so obvious in the Sparrowhawk. It could not be proven that attendance rates of the male increased during the female's most fertile period. This relationship was confused by the diurnal variation in the rates of other behaviours (hunting and display in particular).

The likelihood of fertilization is also affected by the quality and quantity of sperm (Bird and Laguë 1977, for American Kestrel; Wishart 1987). No data on the ejaculate quality of Sparrowhawks were collected, but it is probably similar to that found in Goshawks. Ejaculate volumes of an imprinted Goshawk were usually very small (Berry 1972), and sometimes contaminated with faeces (Corten 1973). Volumes of ejaculates, and the quality and number of sperm per ejaculate in other Falconiformes were low (Corten 1973, 1974; Oliphant pers. comm.), and could be affected by the number of ejaculations/day. There was no difference between the quality of morning and evening ejaculates of Peregrine Falcon *(F. peregrinus)*(Hoolihan and Burnham 1985). In some artificial insemination trials some fertility is achieved with only one insemination (Oliphant pers. comm).

If sperm quality in Sparrowhawks is low, a relatively low level of sperm competition may be suggested (Møller 1988). Despite low quality, the total number of sperm per clutch is greater in species where copulation rates are high and sperm numbers/ejaculate are low than in species which copulate rarely, but whose ejaculate contains many spermatozoa (Møller 1988). Over the course of the season in an established Sparrowhawk pair in which both birds are fertile, the male should deposit enough viable sperm within the female to ensure fertilization of at least part of the clutch. The presence of some infertile eggs suggests that fertilization is not always assured, although 'infertile' eggs may not have been unfertilized, but did not

develop for other reasons (e.g. low shell quality).

The presence of sperm storage tubules (SST's) within the female may further complicate the male's surety of paternity. In Sparrowhawks, most SST's were located in the same area of the female reproductive tract as in the American Kestrel, though they were not as well defined (Bakst and Bird 1987). They were not as numerous as in some other species (Birkhead *et al.* 1990).

The specific function(s) of SST's and their effect on fertility are not well known. In birds which have SST's, the sperm most likely to fertilize is that which is freshest, although the amount of time between copulations by two different males effects the amount of semen stratification, and perhaps the probability of paternity (Birkhead and Hunter 1990). This situation enhances the male's need to limit the female's availability for EPC's, and might encourage the male to seek more copulations from her, particularly after he has been absent (See above).

SST's may have a function of selecting 'better' spermatazoa from the ejaculate (Bakst and Bird 1987), concentrating viable sperm close to the site of fertilization and perhaps increasing fecundity. This function would support the high number of copulations.

Another function of SST's in Sparrowhawks might be to increase the likelihood of fertility in the final eggs of a clutch. Any higher fertility caused by the presence of SST's may be lessened since the quality of eggs in a clutch declines as the number of eggs increase, and suggests a decline in hatchability (Frumkin 1988). In Sparrowhawk, a female might lay up to 7 eggs taking 13 days to do so (Newton 1986). The hen starts incubating the clutch after the first few eggs are laid, thereby being less available for copulations. For the last eggs, stored sperm might be the only sperm within the reproductive tract at the time of ovulation of these last eggs. Further, the presence of a formed egg in the female reproductive tract may inhibit fertilization by sperm introduced after its formation. Stored sperm may be more likely to fertilize some ova produced after the first egg. The effect of the egg-expelling muscular contractions on the storage tubules (Hawkings pers. comm) is a decrease in the number of stored sperm, and may be important if the laying of one egg and ovulation of the next were fairly synchronous. This relationship may affect the number of stored sperm available to fertilize ova ovulated after the first egg. In Sparrowhawks, the regular laying of most eggs in the morning supports the notion of

ovipository-ovulatory synchrony.

Although the functioning of the SST's was not investigated here, paired females that engage in EPC's (and presumably store sperm) do rear the offspring of males other than that of their mates. This storage of sperm may act as a hedge against the possible infertility of her own mate. It might allow her to raise offspring of higher quality if the cuckold is of higher quality than her principal mate. For a breeding male, sperm stored in females other than his mate may act as a hedge against female infertility or late season destruction/desertion of the nest.

These possible functions of the SST's suggest the difference in the number of sperm seen within them could be related to the length of time since their last copulation, the time of day in which the birds were captured, the point at which they were in their laying sequence, and whether they had laid an egg on the day of capture. None of the behavioural data suggest a particular function of the SST's in Sparrowhawks.

Besides making sure of his paternity with his mate, male Sparrowhawks are available to copulate with other females (Fitch and Shugart 1984). EPC's by both sexes occurred in Sparrowhawk, and these produced young (Chapter 5). All EPC's witnessed in Sparrowhawks in Edinburgh occurred between an established male on his nesting territory and an intruding female. Whether the possession of a territory was a measure of the male's likelihood of participating in EPC's was unknown. In other species EPC's are primarily with nearby territorial males (Björklund and Westman 1983; Westneat 1987), and their frequency might depend on population density (Birkhead *et al.* 1985). The preference for neighbouring extra-pair mates was suggested in Edinburgh. There was not a sufficient range of breeding densities to investigate its effect on copulation rates. The number of EPC's that produce young may be related to the egg-date synchrony of the breeding population (See Chapter 5).

In Sparrowhawks, a high quality male that spends more time on his nesting place is presumably more likely to be at home, and therefore more likely to be approached for EPC's. The occasional tolerance by individual breeding Sparrowhawks of intruders of the opposite sex suggests that both sexes are open to other mating opportunities (EPC's or mate replacement). This sex related bias in nesting place defence is seen in other species (Birkhead 1979), and is suggested by sexual selection theory. Unsuccessful polygyny has been reported in Sparrowhawks (Young 1973). Also, Newton (1986) observed several cases where two females shared a nest. The

production of extra-pair offspring suggests that EPC's are successful (Chapter 5).

The likelihood of sexual selection in Sparrowhawks is demonstrated by Newton *et al.* (1981). This selection determines not only the paternity of the young, but the quality of paternal care throughout the breeding season. To pair with a mate of high quality is a goal shared by both male and female. A female which is paired to a high quality male should remain on the nesting place, and copulate with her mate often (particularly during her most fertile periods). This is demonstrated in a crude manner in the Edinburgh Sparrowhawks by examining the behaviours of the replacement birds, and comparing them to those of long established birds. Since the pairs in which replacements occurred were not associated with each other for as long as the established ones, the number of copulations were lower, as was the amount of time spent together. Individual and territory quality probably affected the amount of time the male spends away from the nesting place, a theory untested due to the homogeneity of Sparrowhawk nesting places under observation in this study.

Apart from the behaviours needed to maintain the pair-bond, in order to increase her productivity, a breeding female may also engage in EPC's. For her these may be either a means of ensuring insemination by a fertile male, or enhancing the possibility of cuckoldry by a male of higher quality (Knowlton and Greenwell 1984; Newton 1989). EPC's may also be an attempt to establish herself as the resident female on a territory with a male of better quality than her own. EPC's by breeding females in Edinburgh were probably performed for both purposes. Some authors (Trivers 1972; Fitch and Shugart 1984) suggest there is no advantage gained by the female by engaging in EPC's, because one male is sufficient to inseminate her, and she risks the chance of desertion by her partner. The relative worth and risks of EPC's to individual birds, both male and female, could be related to the reproductive synchrony of the breeding pairs in the population (Birkhead and Biggins 1987).

The larger size of the female, her ability to fly throughout the fertile period, and the lack of a male intromittent organ suggest that she has more control over EPC's and WPC's than the male. It is therefore possible that if a breeding male is of low quality, but within proximity of one (some) of a high quality, his mate may pursue EPC's frequently. The homogeneity of the population examined in Edinburgh did not allow for the examination of this possibility. In Sparrowhawks, female cooperation in both WPC's and EPC's were demonstrated by solicitation calls and postures.

If increased food presentations or guarding by the male ties the female more to the nesting place (or male), her chances of EPC's might be reduced. If these EPC's increase the reproductive potential of that female, the strategies of male and female conflict. Presumably, the more time the male spends guarding the female the less likely she is to engage in EPC's. In Edinburgh the lack of observed EPC's during the days just prior to egg laying may be affected by many factors including increased mate guarding, increased feeding, and increased female commitment to the nest.

Although no link between the seasonal timing of EPC's and fertilization potential could be made, females did engage in EPC's in the morning more often. This situation mimics the pattern for WPC's. The timing of EPC's might be important if fertility is higher in the morning. A similar relationship between intrusion rates and fertilization potential in the female was seen. Intrusion rates increase during the fertile period in other species (Birkhead 1979; Birkhead *et al.* 1988).

The probability that the efficiency of storage is reduced as time passes should not be forgotten when considering that the EPC's observed in Sparrowhawks occurred some days before the female's most fertile time. It may be that SST's are selected for because they enhance within-pair, rather than extra-pair, fertility.

For un-paired birds which are in condition to breed, but cannot because of limitations either in potential mates or on nesting places, entering the breeding population is of prime importance. Two general tactics may be pursued: to wait for an opening at a nesting place due to the death or desertion of the resident, or to oust a resident bird by force. In Edinburgh, Sparrowhawks were known to replace lost breeders, but whether territory-holders were ever evicted could not be proven.

Observations of un-paired individuals trying to enter the breeding population were subject to observational biases. Some further information could be drawn from radio-tagged non-breeders (Chapter 4) early in the season. I could not be certain that the 'non-breeders' did not breed outside of the area where individuals were identifiable, but this was unlikely. The number of intrusions by males vs. females, and yearlings vs. adults was not inconsistent with the seasonal change in activities of breeding birds and the age composition of the breeding population, but may have been confused by breeding asynchrony in the urban population.

Observations of 'breeding' behaviours of un-paired individuals were relatively rare.

When they did occur, they were probably the result of attempts to enter the breeding population, and may have been directed at a particular potential mate or territory. Alternatively, these behaviours could also have functioned as means of engaging in EPC's.

There were no observations of EPC's by un-paired males. If they do occur their advantage (beyond the establishment of a pair-bond) would be to allow males to produce off-spring without having to care for the female and/or the growing brood.

Both breeding and non-breeding male intruders were tolerated at times by the female on the territory. In as much as territory holding may reflect the male's quality, established females may be unwilling to copulate with an intruder whose quality she cannot assess, thus risking lowered productivity (particularly as long as her mate was healthy and there were other territory holding males in the area). Still, the tolerance by some breeding females of intruding male non-breeders may indicate that females were leaving their breeding options open. Although I never observed a breeding female receiving food from an intruding male, this might be another reason for tolerating an intruding male. A male intruder could not always be sure of a female's intentions, and may risk predation by approaching for EPC's, but may gain useful experience.

As with the male, for an unpaired female EPC's may function in establishing her with a territory holding male. Also, EPC's might provide an unpaired female with an added chance of producing offspring if she is able to find a male and attempt to nest later in the season. A female which attempts to breed later in the season probably pairs with either a male of lesser quality, or replaces an established female. In either case late breeding decreases productivity (Newton and Marquiss 1984). Sperm of a higher quality male stored in the female might increase productivity or the quality of the offspring (See discussion of SST's above).

Unpaired females were tolerated by territory holding males and might have engaged in EPC's. Typically, these were females which were not identified. In one case a non-breeding, yearling female became the mate of the male after engaging in EPC's with him. The fate of the adult female she eventually replaced was unknown, but after the observation of EPC's, aggressive chases between the replaced- and replacement females were seen. In one instance a female which was not a known breeder received food from a territory-holding, paired male. Whether this was an attempt to

gain EPC's from the intruder was unknown, but no EPC followed.

The intrusion onto the territory by non-breeders of both sexes was higher in the morning and may have been linked to female fertility or coincidental to hunting activity by these individuals

Whether plumage differences between yearlings and adults were related to the tolerance by breeders was unknown. Plumage differences have been suggested as an adaptation which allows yearlings to approach nesting places more closely (Stephenson and Stewart 1943). If a breeding place becomes available, the yearling is close by as a potential replacement. Plumage differences between adult and yearlings may also have been used to assess the quality of a potential EPC partner by breeders. The fact that many more adult Sparrowhawks breed than yearlings indicates that there is selection or competition for adults as breeders (Newton 1986), but the behaviours surrounding the replacement of an adult female by a yearling suggest that plumage is not a totally reliable assessment of an individual's ability to occupy a territory.

Nest building, display and defense, and vocalization behaviours (among others) of both paired and unpaired Sparrowhawks were highly variable. Their inclusion in this analysis is primarily to represent the nature of the other breeding behaviours which are perhaps not as illustrative of the reproductive strategies in Sparrowhawks. The high degree of variability does not imply that these activities are unimportant to breeding success, just that their effect is more difficult to assess.

In general, all breeding behaviours seemed to change over the season, with activity increasing as the egg-date approached, and culminating at or around that time. All behaviours exhibited a diurnal pattern with periods of activity in the morning and to a lesser extent in the evening. The middle of the day was spent roosting, and loafing. This general pattern and the specifics of nest building, and display and defense are consistent with the reports of Owen (1916), Cramp and Simmons (1980), and Newton (1986). Behaviours were probably dependent on many factors including weather, competition for nesting places, age and experience of the breeders, time of day and season, and the reproductive states of the birds.

Nest building in Sparrowhawks showed a high degree of variability in effort. Unlike most other raptors (Newton 1979), the nest structure is built mostly by the

female, although the male initiates most of the building bouts. Perhaps in this manner, the female is easier for the male to guard. A more direct function of the nest and its building on the reproductive success of the breeding pair was to provide the female with a safe place for eggs and brood. It may also helped to cement the pair-bond. No simple relationship existed between the aspects of nest building behaviour examined here, and the success of Sparrowhawk pairs.

The importance of display and defence in ensuring reproductive success cannot be over-emphasized. Display probably functions in advertising the availability of an individual to breed, in maintaining the pair-bond, and excluding rival birds from the territory.

As in other behaviours, the motivations of displaying male and female Sparrowhawk may be in conflict, although this is not always so. However, as in other behaviours, the advantages of a stable pair in the reproductive effort are much more important than extra-pair associations. It should be assumed that in general, the behaviours of Sparrowhawks promote pair formation and pair stability throughout the breeding season.

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Appendix 1, Table 1.1 List of common and scientific names of plants and animals mentioned in the text.

MAMMALS

Bank vole	*Clethrionnomys glaveolus*
Squirrel(grey)	*Sciurus carolinensis*

BIRDS

Mallard	*Anas platyrhynchos*
Osprey	*Pandion haliaetus*
Red Kite	*Milvus milvus*
Black Kite	*M. migrans*
Black-shouldered Kite	*Elanus caeruleus*
Mississippi Kite	*Ictinia mississippiensis*
European Sparrowhawk	*Accipiter nisus nisus*
Shikra	*A. badius*
Levant Sparrowhawk	*A. brevipes*
Goshawk	*A. gentilis*
Sharp-shinned Hawk	*A. striatus*
Cooper's Hawk	*A. cooperi*
Buzzard	*Buteo buteo*
Red-tailed Hawk	*B. jamacensis*
Swainson's Hawk	*B. swainsoni*
Ferruginous Hawk	*B. regalis*
Honey Buzzard	*Pernis apivorous*
Golden Eagle	*Aquila chrysaetos*
Black Eagle	*A. verreauxi*
Egyptian Vulture	*Nephron percnopterus*
Hen/Northern Harrier/Marsh Hawk	*Circus cyaneus*
Peregrine Falcon	*Falco peregrinus*
Eleonora's Falcon	*F. eleonorae*
Hobby	*F. subbuteo*
Merlin	*F. columbarius*
Eurasian Kestrel	*F. tinnunculus*
American Kestrel	*F. sparverius*
Woodcock	*Scolopax rusticola*
Pheasant	*Phasianus colchicus*
Feral Pigeon	*Columba livia*

Wood Pigeon	*C. palumbus*
Collared Dove	*Streptopelia decaocto*
Tawny Owl	*Strix aluco*
Magpie	*Pica pica*
Rook	*Corvus frugilegus*
Crow	*C. corone*
American Crow	*C. brachyrhynchos*
Swift	*Apus apus*
White Wagtail	*Motacilla alba*
Waxwing	*Bombycilla garrulus*
Dunnock	*Prunella modularis*
Whitethroat	*Sylvia communis*
Blackcap	*S. atricappila*
Willow Warbler	*Phylloscopus trochilus*
Chiffchaff	*P. collybita*
Goldcrest	*Regulus regulus*
Robin	*Erithacus rebecula*
Blackbird	*Turdus merula*
Fieldfare	*T. pilaris*
Redwing	*T. iliacus*
Song Thrush	*T. philomelos*
Mistle Thrush	*T. viscivorous*
Coal Tit	*Parus ater*
Great Tit	*P. major*
Blue Tit	*P. caeruleus*
Wren	*Troglodytes troglodytes*
Brambling	*Fringilla montifringilla*
Chaffinch	*F. coelebs*
Goldfinch	*Carduelis cardeulis*
Greenfinch	*C. chloris*
Bull Finch	*Pyrrhula pyrrhula*
Tree Sparrow	*Passer montanus*
House Sparrow	*P. domesticus*
Starling	*Sturnus vulgaris*
Budgeriegar	*Melopsittacus undulatus*
Cockatiel	*Leotolophus sp.*
Cockatoo	*Kakatoë sp.*

PLANTS

Cedar	*Thuja sp.* or *Cedrus sp.*
European Larch	*Larix decidua*
Sitka Spruce	*Picea sitchensis*
Scot's Pine	*Pinus sylvestris*
Willow	*Salix sp.*
Alder	*Alnus sp.*
Sycamore	*Acer pseudoplatanus*
Chestnut	*Aesculus sp.*

Appendix 1, Table 3.1 Post-mortem findings and pollutant levels of Sparrowhawks found in and around Edinburgh 1986-1989.

Ref. No.	Age	Sex	Year	Death	% Lipid in Liver	pp' DDE	Dieldrin	HCB	PCB	Merc.
8535*	J	M	'86	Shot	6.43	10.24	0.65	---	3.95	2.65
8860	J	M	'86	Car	2.68	0.43	0.32	---	1.20	0.36
8861	A	F	'86	Pred.	2.53	8.68	2.31	---	3.47	4.36
9151*	J	M	'84	Falc.	2.98	1.56	0.96	0.09	2.03	none
9152	J	M	'87	Starve	3.27	6.20	0.92	---	2.26	2.61
9153	J	M	'87	Pred.	3.62	---	---	---	0.35	0.67
9166*	J	F	'87	Unkn.	2.99	2.31	0.75	---	12.21	1.82
9168L*	J	M	'87	Unkn.	2.98	1.80	0.34	---	2.48	4.14
9169L	J	F	'87	Unkn.	2.89	0.29	0.20	---	0.67	1.29
9170L	J	M	'87	Unkn.	3.01	0.64	0.21	---	5.12	1.60
9171L	A	M	'88	Unkn.	2.87	5.12	0.53	0.07	28.42**	2.32
DDE is from DDT					3.29±0.32	3.72±1.14	0.72±0.2	0.08±0.01	5.65±2.48	1.98±0.43

HCB = Hexachlorobenzene

PCB = Polychlorinated biphenyls

* - Birds from area surrounding specific study area (primarily rural).

**r_{21} = 0.856, $\alpha < 0.01$; Dixon's test for outliers

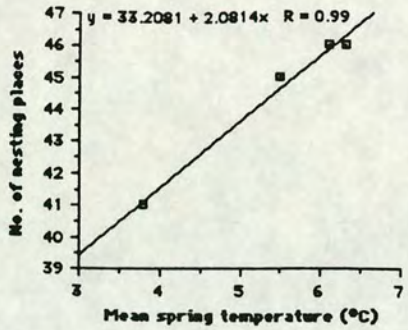
Appendix1, Table 4.1 Age sex and duration of radio-tracking of Sparrowhawks fitted with radio-transmitters in Edinburgh, 1987 and 1988 (Age: A=adult, Y=yearling; Sex: M=male, F=female).

Ring number	Age	Sex	Date transmittered	Duration in days (no. of fixes)
DA53776	A	M	15-02-87	81 (187)
DA53778	A	M	13-03-87	53 (67)
DA53779	A	M	17-03-87	68 (63)
DA28560	A	F	18-03-87	63 (119)
EN28600	Y	F	07-10-87	54 (39)
EN28577	A	F	16-11-87	77 (58)
DA53770	A	M	22-11-87	18 (24)
EN51082	Y	F	24-11-87	61 (53)
DA53716	Y	M	06-12-87	4 (12)
EN28592	Y	F	12-02-88	73 (93)
DA53718	A	M	14-02-88	68 (67)
DA53792	Y	M	25-02-88	52 (69)
DA53719	Y	M	25-02-88	80 (145)
DA53712	Y	M	02-03-88	71 (118)
DA53720	Y	M	02-04-88	26 (59)
DA53780	A	M	02-04-88	32 (27)
DA53755	Y	M	18-04-88	54 (42)
DA53714	Y	M	22-11-88	56 (24)
DA53715	Y	M	27-11-88	27 (26)

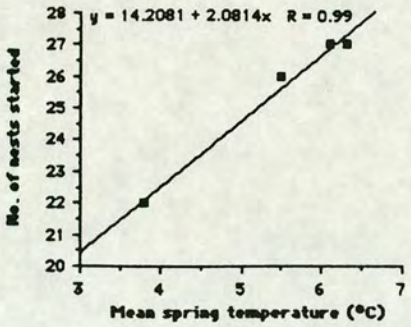
Appendix 1, Table 5.1 List of parameters measured at nesting places of Sparrowhawks in Edinburgh, 1986-1989.

Woodsize	Area of wood containing nest tree
Woodcomp	Composition of nest site wood: Conifer, Mixed or Broad-leaved
Tree	Species of nest tree
Treeht	Height of nest tree in metres
Cbh	Circumference of nest tree at breast height in centimetres
Nstht	Height of nest in meteres
Pnstht	Percentage nest height (Nstht/Treeht x 100)
Congt5	Number of coniferous trees > 5 m tall in 10 m radius plot centred on nest tree
Decgt5	Number of deciduous trees > 5 m tall in 10 m radius plot centred on nest tree
Conlt5	Number of coniferous trees < 5 m tall in 10 m radius plot centred on nest tree
Congt5	Number of deciduous trees > 5 m tall in 10 m radius plot centred on nest tree
Treegt5	Number trees > 5 m tall in a10 m radius plot centred on nest tree (Congt5 + Decgt5)
Treelt5	Number of trees < 5 m tall in 10 m radius plot centred on nest tree (Conlt5 + Declt5)
Shrub	Percentage of 10 m plot centred on nest tree covered by shrubs (woody perennial, usually < 5 m tall, with branches from the ground upward); 4 categories: 0%, <5%, 5-25%, >25%
Disturbance	Index of human disturbance; Low, Medium, High
Distdist	Distance to nearest regular human disturbance; road, path, building, etc.

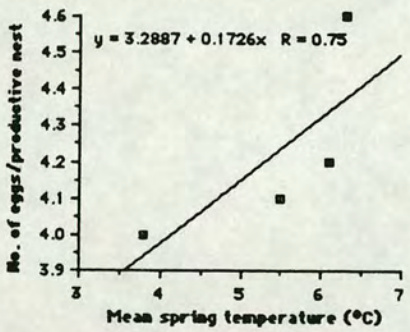
Appendix 1, Figure 5.1 Effect of weather on Sparrowhawk production in Edinburgh, 1986-1989.



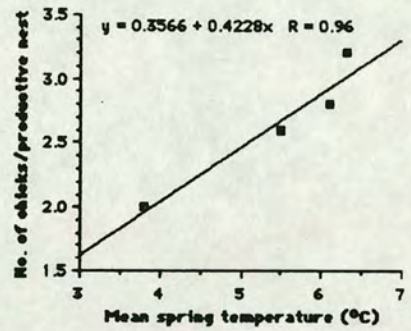
c) Number of eggs/productive nest in relation to mean spring temperature.



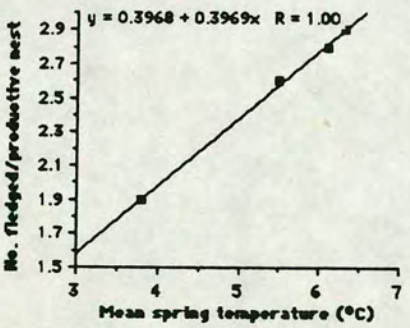
d) Number of chicks/productive nest in relation to mean spring temperature.



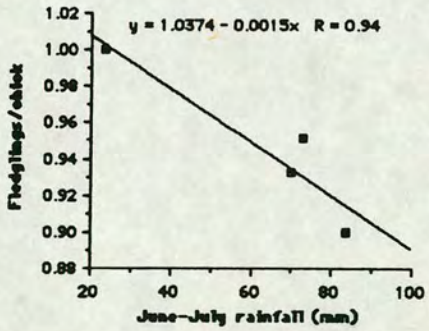
e) Number of fledglings/productive nest in relation to mean spring temperature.



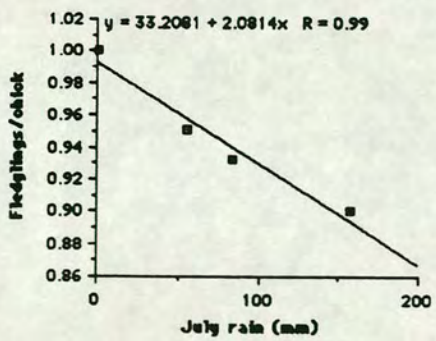
f) Number of fledglings/chick hatched in relation to mean rainfall in June and July.

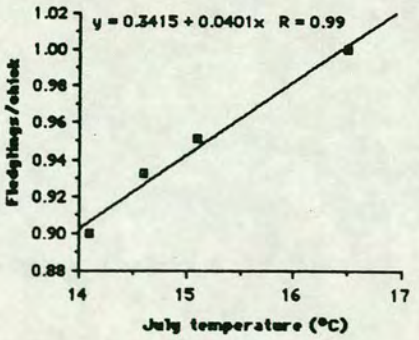


g) Number of fledglings/chick hatched in relation to July rainfall



h) Number of fledglings/chick hatched in relation to July temperature.





Appendix1, Table 5.2 Results of examination of unhatched Sparrowhawk eggs (including shell indecies) in Edinburgh, 1986-1989.

Ref.no.	Site	Development	% Lipid of egg	Shell thickness index
E2805	0034	Cracked, small dev.	7.00	1.27
E2806	0039	Cracked, small dev.	6.36	-
E2807	0004	Cracked	23.47	1.43
E2808	0042	Cracked	6.05	1.49
E2809	0038	1/4 embryo	6.80	1.39
E2810	0038	Cracked, small dev.	-	-
E2811	0038	Cracked, small dev.	-	1.17
E2812	0008	No development	7.32	1.39
E2813	0008	Thin Cream	-	1.35
E2814	0022	Cracked, small embryo	-	1.45
E2815	0022	Thick cream	5.66	1.23
E2816	0037	Thick Cream	7.93	1.49
E2817	0040	Cracked, no develop.	-	1.19
E2818	0040	Cracked, no develop.	6.90	1.22
E2819	0040	Cracked, thin cream	-	1.09
E2423	0021	Cracked, creamy	3.05	-
E2424	0001	Small develop.	6.18	1.39
E2425	0037	Addled	5.50	1.26
E2426	0022	Small develop.	7.55	1.16
E2427	0035	Small develop.	5.42	1.30
E2428	0020	Thick cream, no dev.	6.72	1.56
E2429	0034	Addled	33.56	1.27
E2430	0008	Cracked, small embryo	-	1.24
E2431	0023	Small develop.	6.75	1.37

Appendix 1, Table 5.3 Pollutant levels in Sparrowhawk eggs in Edinburgh, 1986-1989. (Organochlorine conc.: ppm wet weight (in lipid))

Ref. No.	Site	HCH	HCB	HEOD	pp' DDE	PCB	Mercury	HE
E2805	0034	-	-	0.45	1.77	13.10	0.77	-
E2806	0039	-	0.16	1.06	2.70	37.82	0.56	-
E2807	0004	-	0.18	1.85	13.05*	49.80	0.95	-
E2808	0042	-	-	0.78	3.76	29.64	0.56	-
E2809	0038	-	-	0.55	2.54	13.45	0.33	-
E2810	0038	-	-	-	-	-	-	-
E2811	0038	-	-	-	-	-	-	-
E2812	0008	0.08	-	0.64	2.69	12.03	0.48	-
E2813	0008	-	-	-	-	-	-	-
E2814	0022	-	-	-	-	-	-	-
E2815	0022	-	-	0.57	3.59	20.02	0.62	-
E2816	0037	-	0.08	1.87	3.23	17.62	0.21	-
E2817	0040	-	-	-	-	-	-	-
E2818	0040	-	-	0.62	5.17	2.97	0.60	-
E2819	0040	-	-	-	-	-	-	-
E2423	0021	-	-	0.78 (25.29)	2.51 (81.61)	13.27 (431.03)	0.482	0.37 (12.07)
E2424	0001	-	-	0.85 (13.59)	2.20 (35.28)	12.52 (200.65)	none	0.46 (7.44)
E2425	0037	-	-	3.35 (61.00)	3.81 (69.21)	14.91 (271.26)	0.08	0.50 (9.09)
E2426	0022	-	-	1.33 (17.77)	3.49 (46.39)	17.43 (231.02)	0.361	0.52 (6.93)
E2427	0035	-	-	0.62 (11.35)	13.47 (246.10)**	6.66 (121.23)	0.430	0.28 (5.32)
E2428	0020	-	-	1.69 (25.00)	5.28 (77.53)	22.66 (333.2)	1.16	0.64 (9.49)
E2429	0034	-	-	0.77 (14.90)	2.83 (54.97)	5.84 (306.95)	0.667	0.58 (11.26)
E2430	0008	-	-	-	-	-	-	-
E2431	0023	-	-	1.46 (21.51)	4.60 (67.44)	11.78 (172.97)	0.638	0.32 (4.65)
HCH is from lindane			0.14±0.03	1.13±0.18	4.51±0.83	18.32±2.78	0.52±0.07	0.46±0.04

HCB = hexachlorobenzene

HEOD is from aldrin and dieldrin, PCB = polychlorinated biphenyls, HE = heptachlor epoxide, DDE is from DDT.

*r_{22} = 0.739, α <0.01; **r_{22} = 0.749, α<0.01; Dixon's test for outliers.

Appendix 1, Table 6.1 Behaviours observed in breeding Sparrowhawks in Edinburgh, 1986-1989.

Nest building
- 001 Taking material to nest
- 002 Going to nest w/out material
- 003 Cup formation
- 004 Arrangement of nest
- 005 Remove material from nest
- 006 Picking twigs

Copulation
- 010 unsuccessful w/in pair
- 011 successful w/in pair
- 012 Solicitation w/in pair
- 013 unsuccessful extra-pair
- 014 successful exta-pair
- 015 Extra-pair solicitation

Feeding
- 020 Plucking
- 021 Feeding
- 022 Casting
- 023 Feaking, cleaning toes
- 024 Caching

Presentation of food
- 030 Arrival w/ prey
- 031 Taking prey from male
- 032 Carrying prey
- 033 Fly to nest w/ prey
- 034 Fly from nest w/ prey

Hunting
- 040 Successful witnnessed hunting
- 041 Unsuccessful witnessed hunting
- 042 Still-hunting
- 043 Successful unwitnessed hunting
- 044 Unsuccessful witnessed hunting

Defense
- 050 Aerial defense against intruder on the ground
- 051 Aerial defense against intruder in the air
- 052 Aerial defense against perched intruder
- 053 Defense agains mammalian intruder
- 054 General aerial defense

Relaxing
- 060 Loafing
- 061 Preening
- 062 Sleeping
- 063 Perching
- 064 Roosting

Vocalization
- 070 for unknown reason
- 071 associated with food
- 072 associated with breeding
- 073 associated with defense
- 074 associated with nest building

Coming and going
- 080 Arriving after unknown activity
- 081 Leaving for unknown reason
- 082 Arrival after hunting
- 083 Leaving to hunt
- 084 Leaving due to disturbance
- 085 Leaving to defend
- 086 Arrival to defend

Flying
- 090 Soaring
- 091 Flying in nest area
- 092 Displaying with another hawk
- 093 General flying
- 094 Displaying alone

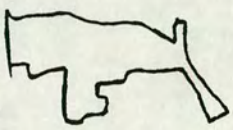
Egg laying
- 100 Incubating
- 101 Settling on eggs
- 102 Laying
- 103 Sitting low in nest
- 104 Perching on nest
- 105 Arrangement of eggs

General
- 110 Unknown activity

Appendix 2: Maps of the study area (Figures 4.1 and 4.2) as well as maps of the ranges of individual Sparrowhawks in Edinburgh (Figures 4.3-4.21). Figure 4.22 illustrates the amount of overlap of the territorties of neighbouring, breeding, adult male Sparrowhawks.The scale is given at the botton of each page. North is marked for each map. For the maps of the study area as a whole, landmarks are included and labled. In the individual range maps, relatively large areas of open ground and areas of woodland are marked. Details accompany each map.

Legend:

= water.



= open ground.

= woodland.

= open ground within the range.

= mixed areas within the range, including built-up areas, small gardens, roads, etc.

NP = nesting place.

NP =nesting place of individual whose range is described by the map.

Ⓡ =roosting site of non-breeders, and remote-roosting breeders. Unless otherwise indicated, roost sites are at the nesting place.

Appendix 2, Figure 3.1 Edinburgh study area 1986-1989.

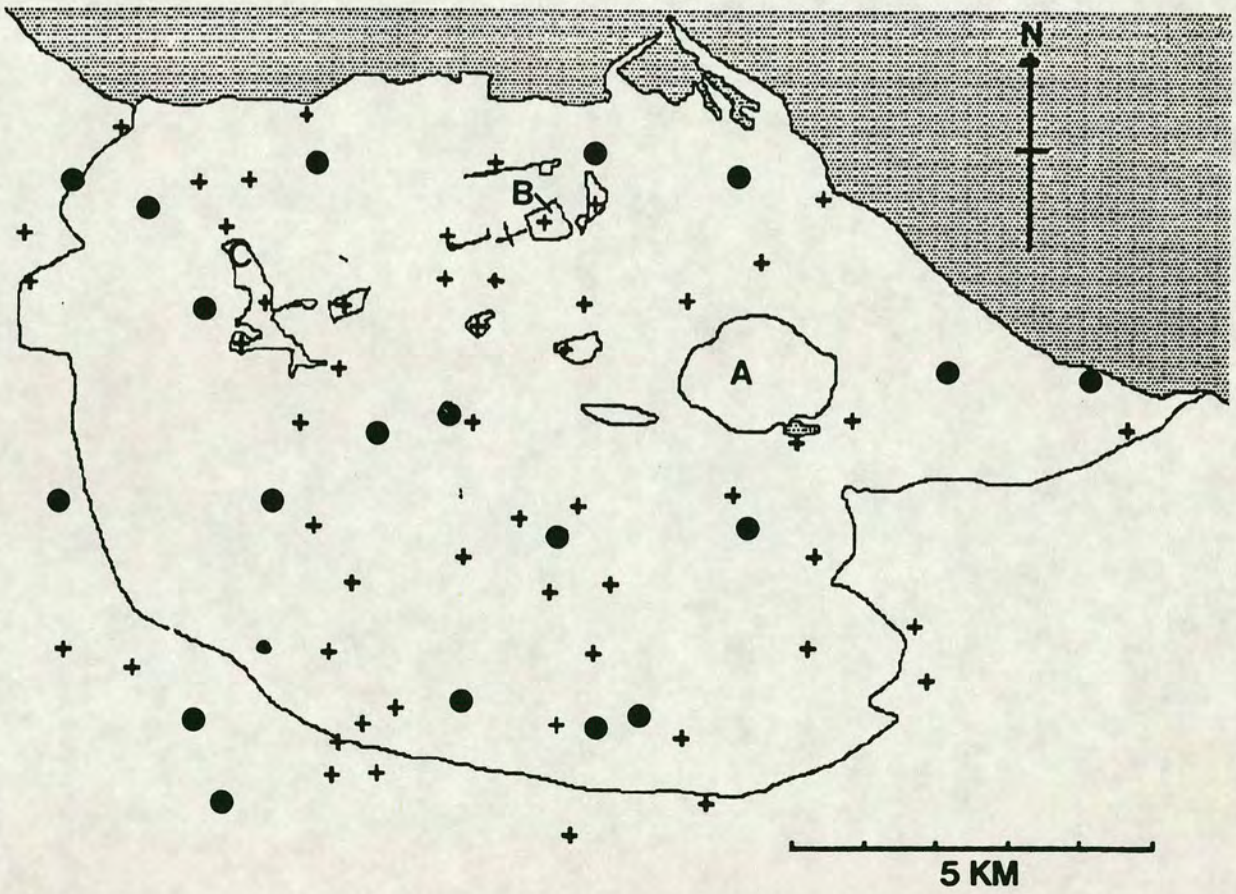
'+' = nesting places which were occupied during or just prior to the study period.

'●' = potential nesting places (determined by presence of trees and distance from occupied nesting place.

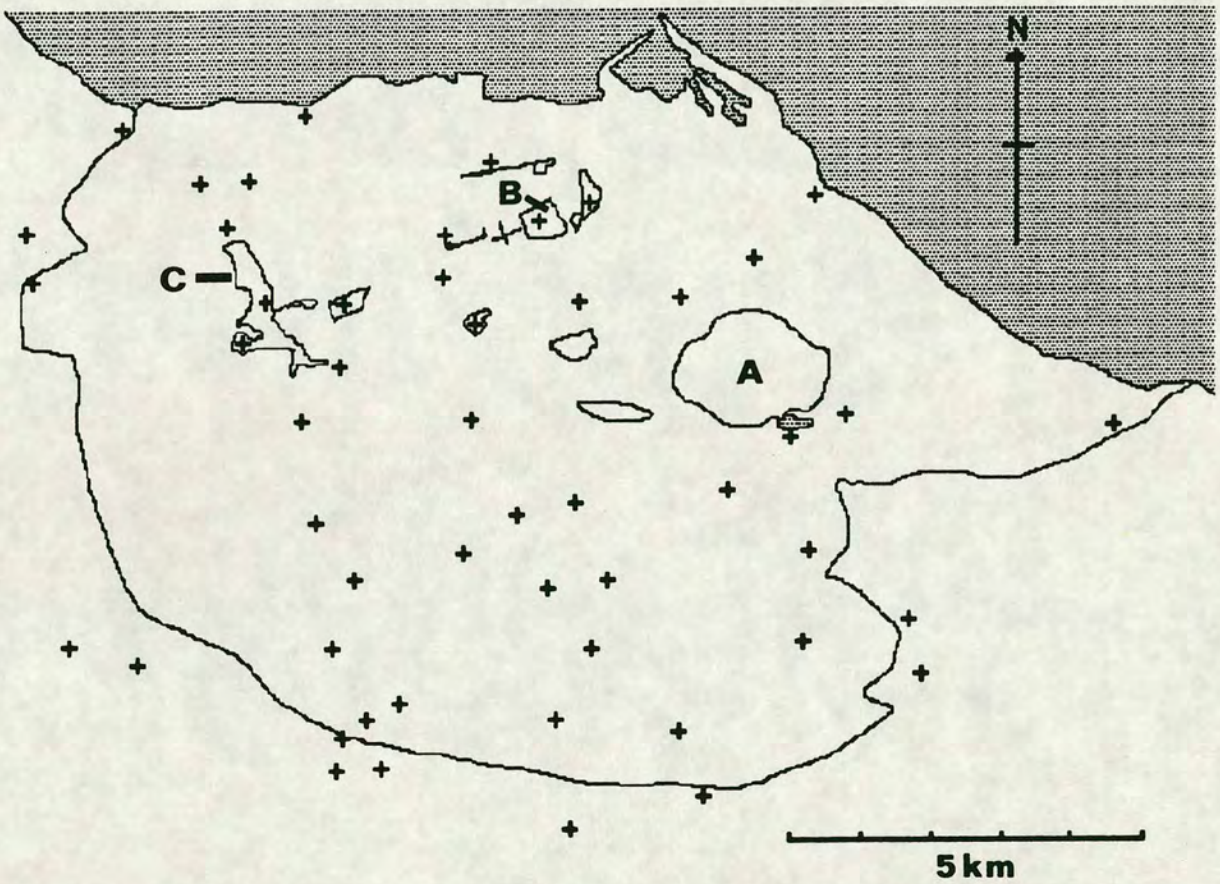
'A' = Arthur's Seat.

'B' = Royal Botanic Gardens.

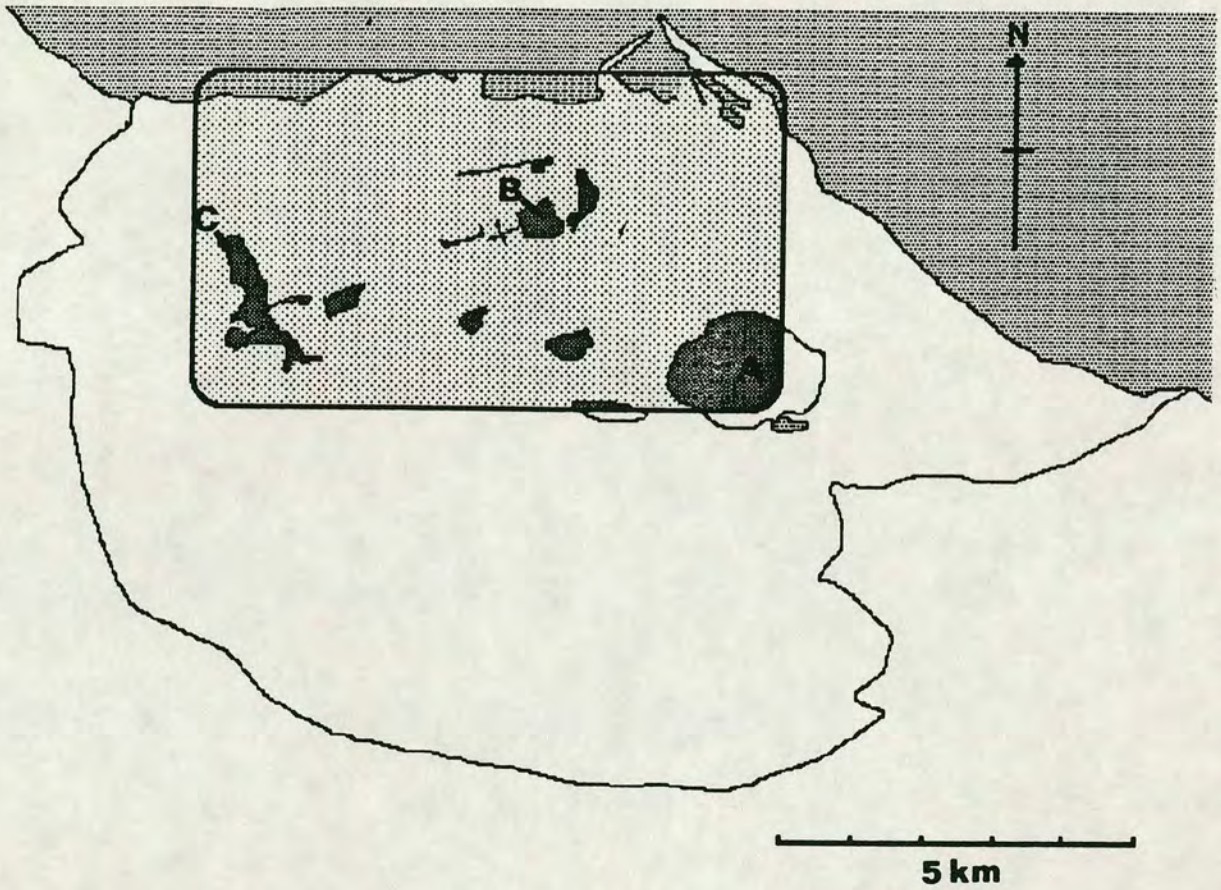
'C' = Corstorphine Hill.



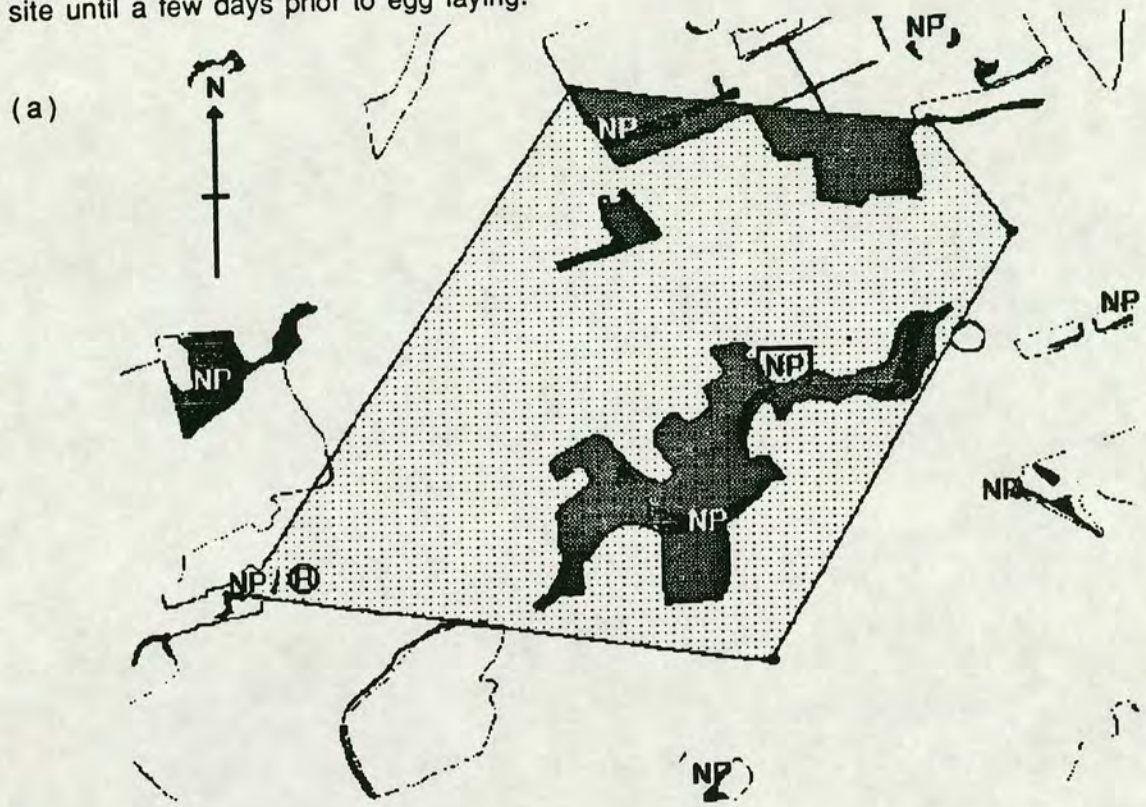
Appendix 2, Figure 4.1 Edinburgh study area, 1986-1989. ('+' = nesting places which were occupied during or just prior to the study period). Some large wooded and open areas included as points of reference (A=Arthur's Seat; B=Royal Botanic Gardens; C=Corstorphine Hill). Scale shown.

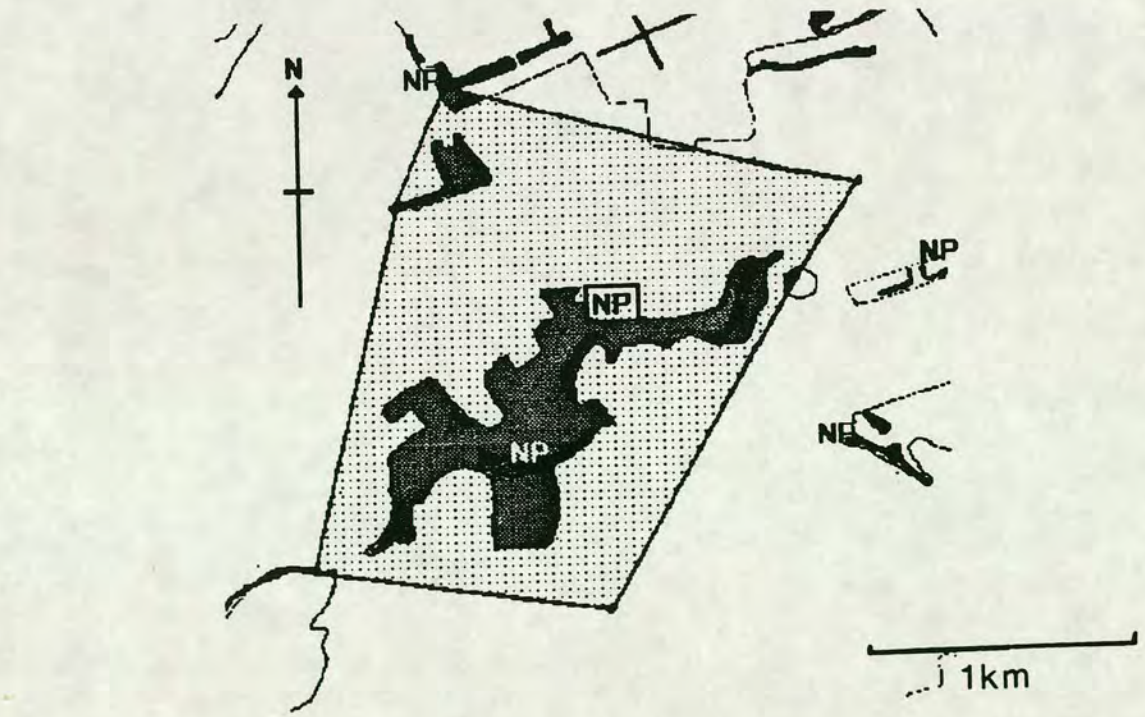


Appendix 2, Figure 4.2 Map of area within Edinburgh (shaded) in which all radio-tracked birds were captured. Some large wooded and open areas included as points of reference (A=Arthur's Seat; B=Royal Botanic Gardens; C=Corstorphine Hill). Scale shown.

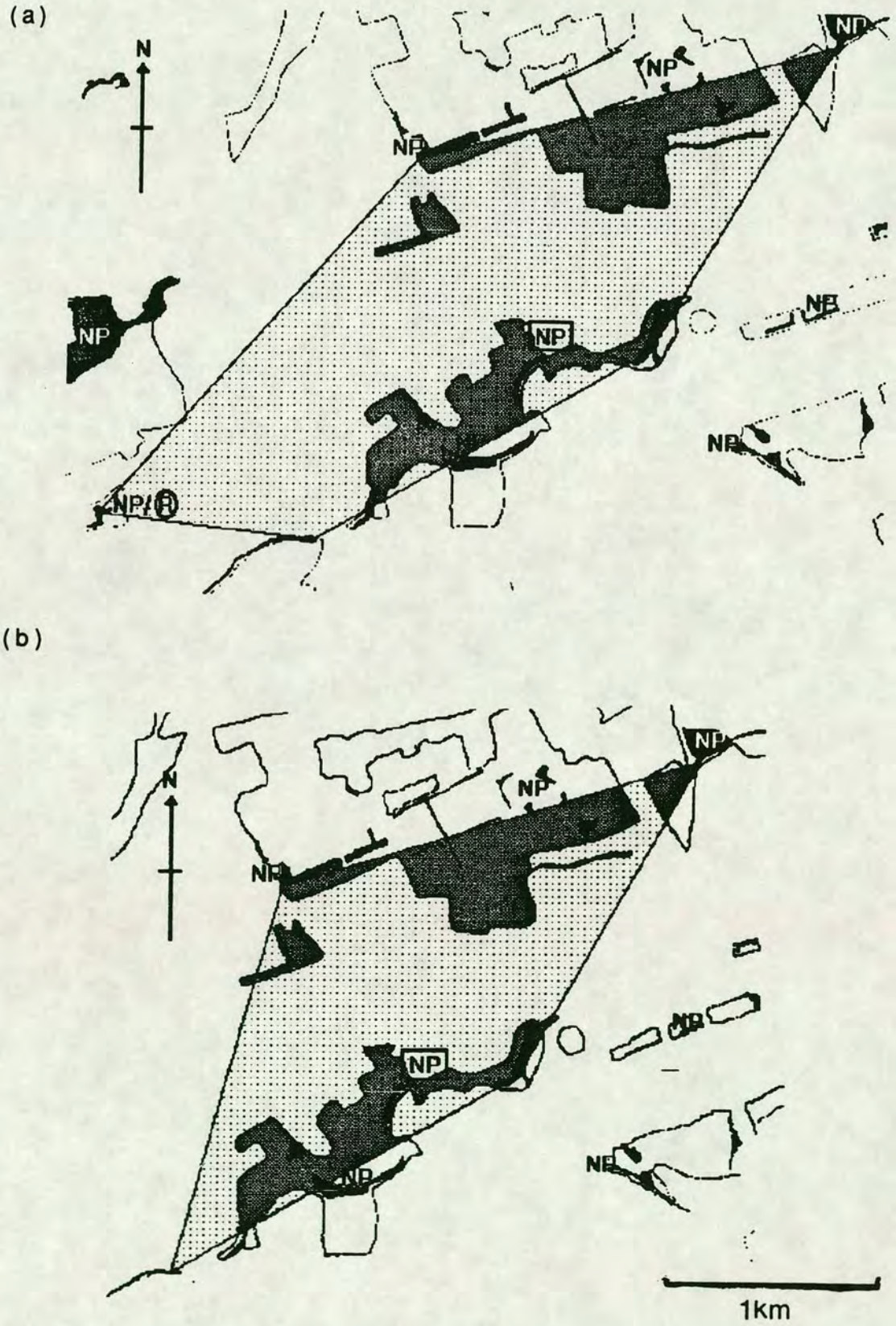


Appendix 2, Figure 4.3 Ranges of a breeding, adult male Sparrowhawk in Edinburgh tracked 02 April - 5 May 1988; (a) range (483 hectares) 02 April - 18 April, including remote roosting site, (b) range (313 hectares) 19 April - 5 May, after principal remote roost was abandoned for a roost at the nesting place. This male was paired with an adult female until his death for unknown reasons on 05 May. He was replaced by a yearling (Figure 4.4) which roosted at the same remote site until a few days prior to egg laying.

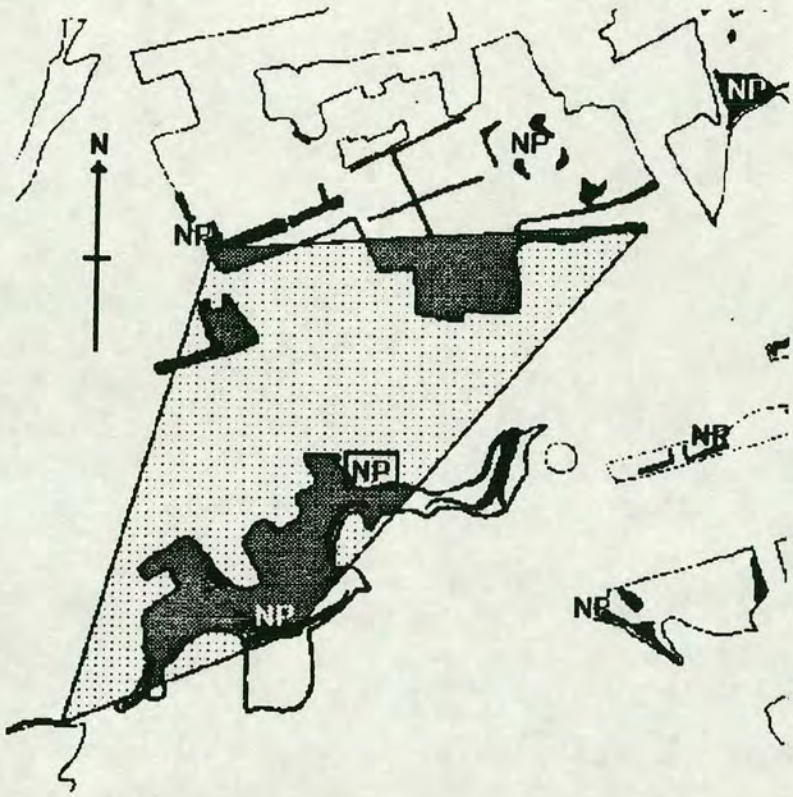




Appendix2, Figure 4.4 Ranges of a breeding, yearling male Sparrowhawk in Edinburgh tracked 18 April - 2 June 1988. This individual replaced a territory holding, adult male (Figure 4.3); (a) the range (418 hectares) prior to, and just after replacing breeder (18 April - 11 May), (b) the range (292 hectares) excluding the remote roost (18 April - 11 May), and (c) the range (246 hectares) after moving principal roosting site to the nesting place (11 May - 2 June).

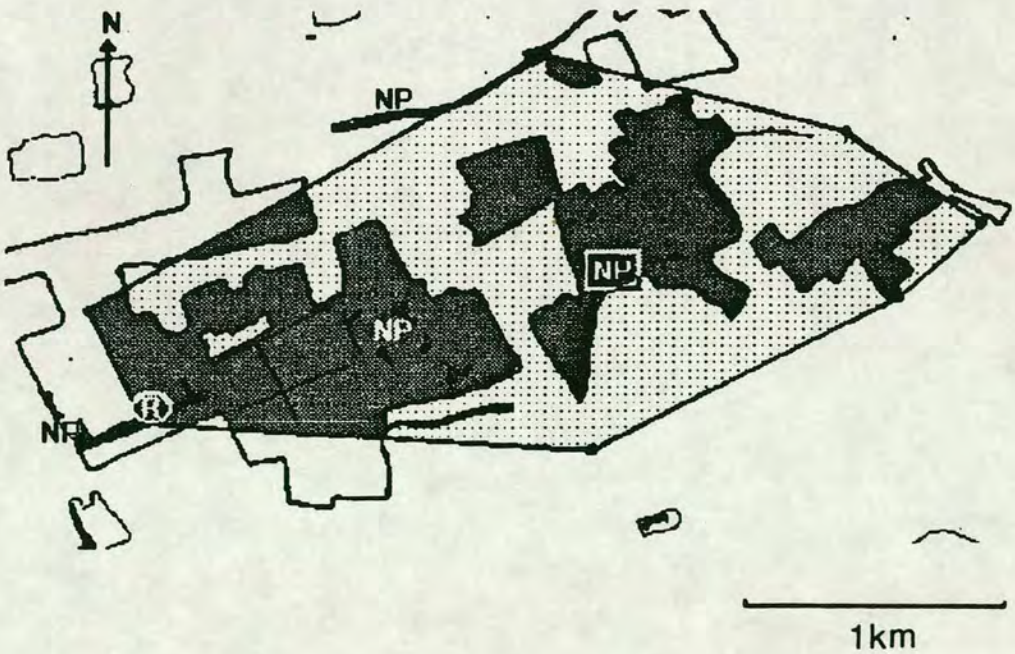


(c)

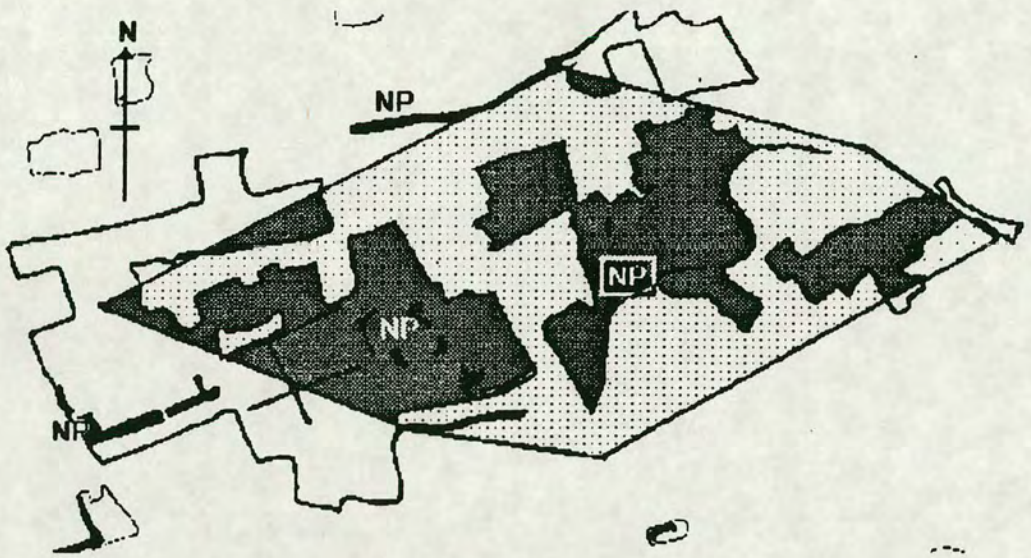


Appendix 2,Figure 4.5 Ranges of a breeding, adult male Sparrowhawk in Edinburgh tracked 17 March-24 May 1987; (a) range (372 hectares) including remote roosting site early in breeding season, 17 March-10 April, (b) range (336 hectares) excluding remote site in early breeding season, (c) range (212 hectares) later in the pre-nesting period, 11 April-2 May. This male paired with an adult female.

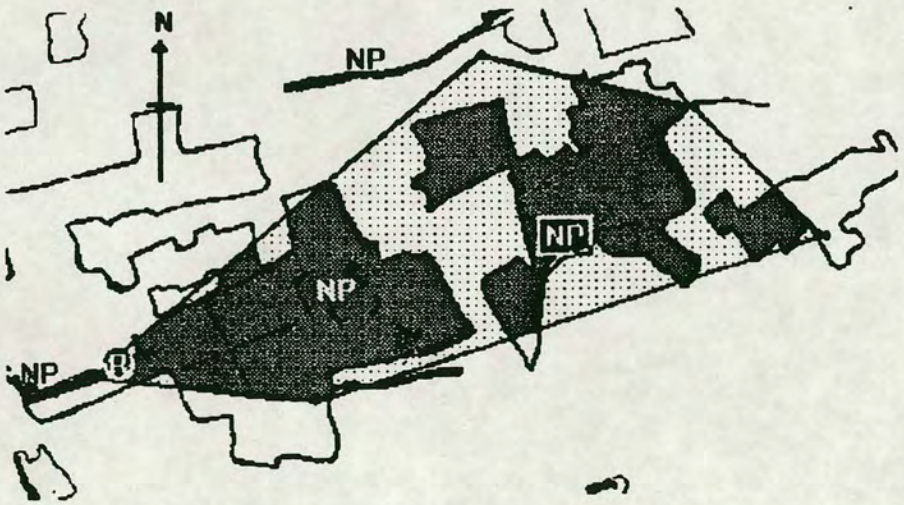
(a)



(b)

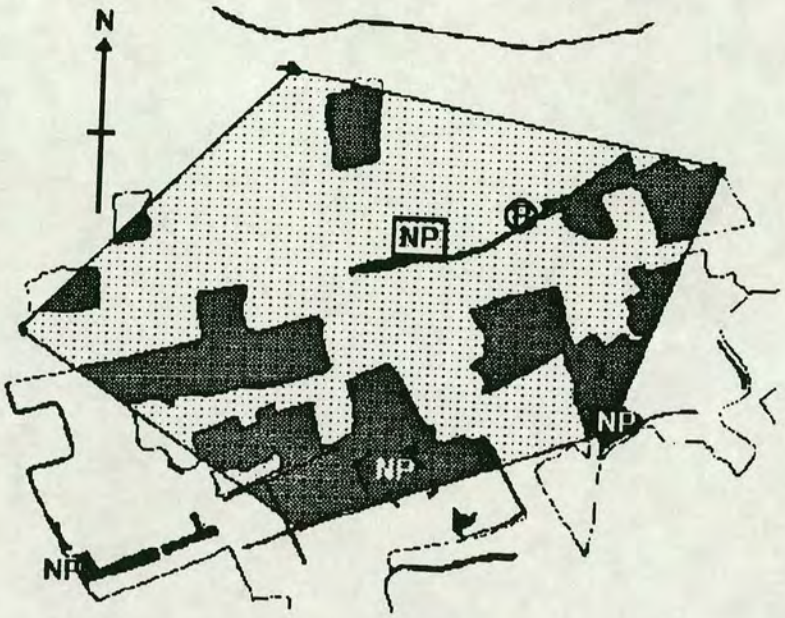


(c)

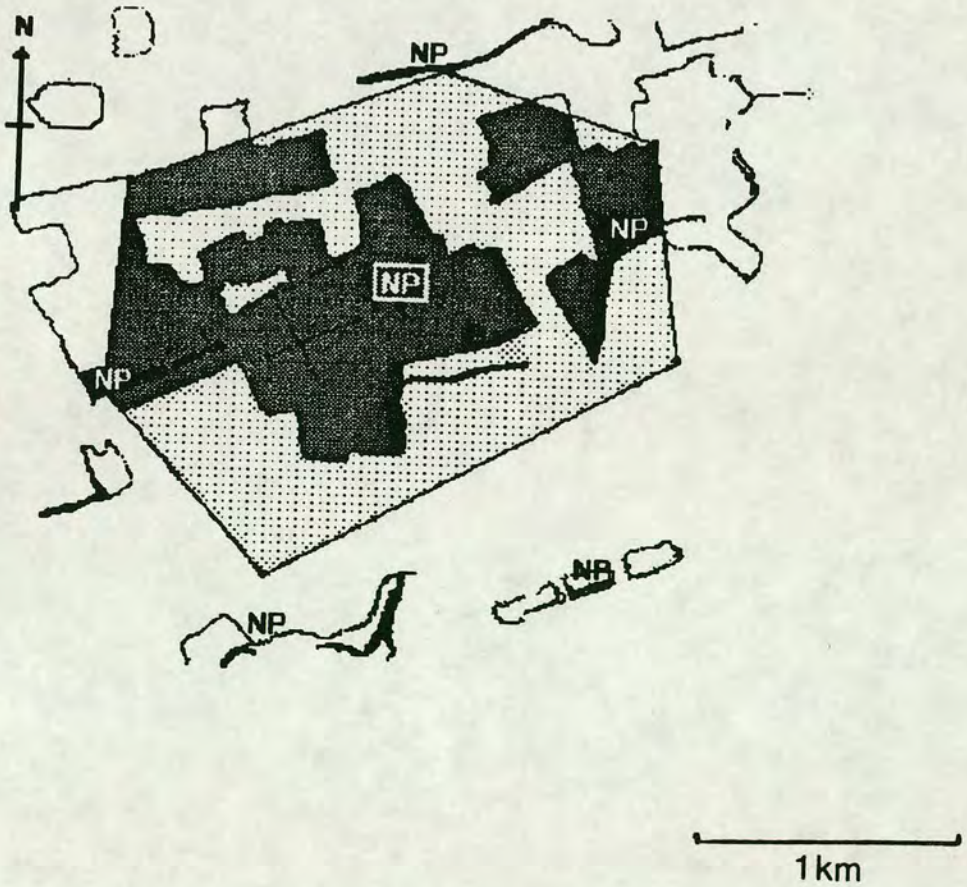


1km

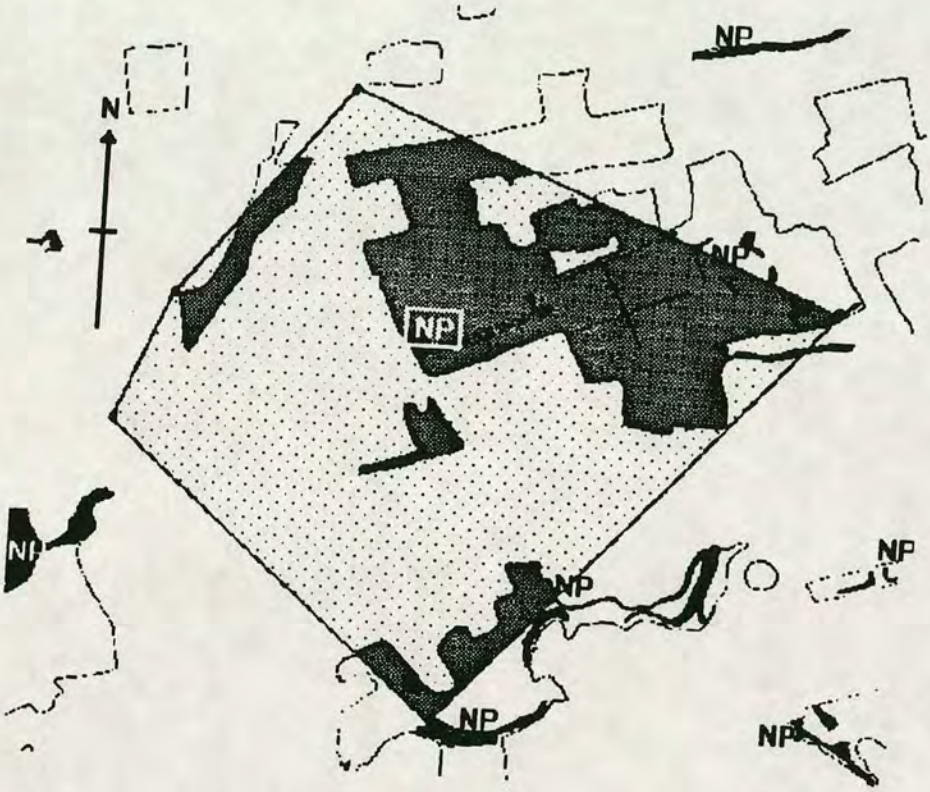
Appendix2, Figure 4.6 Range (350 hectares) of a breeding, adult male Sparrowhawk in Edinburgh, tracked 14 February - 23 April 1988. The nest failed at the egg stage during bad weather.



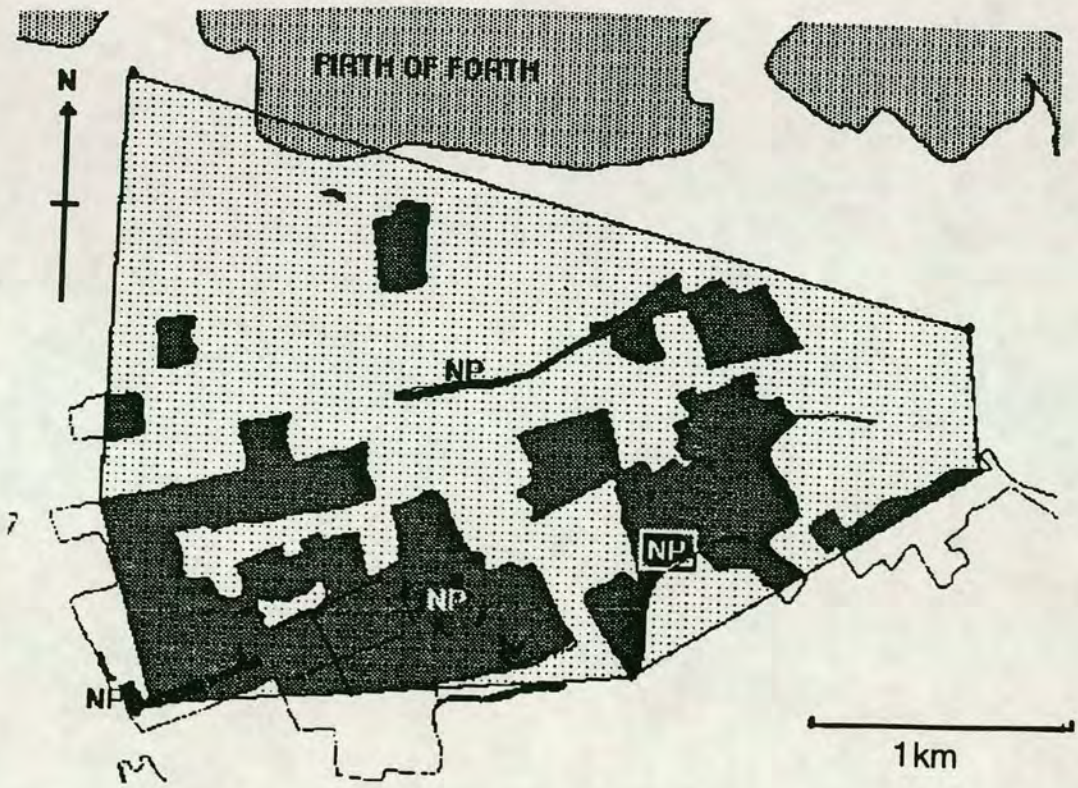
Appendix 2, Figure 4.7 Range (357 hectares) of a breeding, adult male Sparrowhawk in Edinburgh tracked 15 February - 07 May 1987.



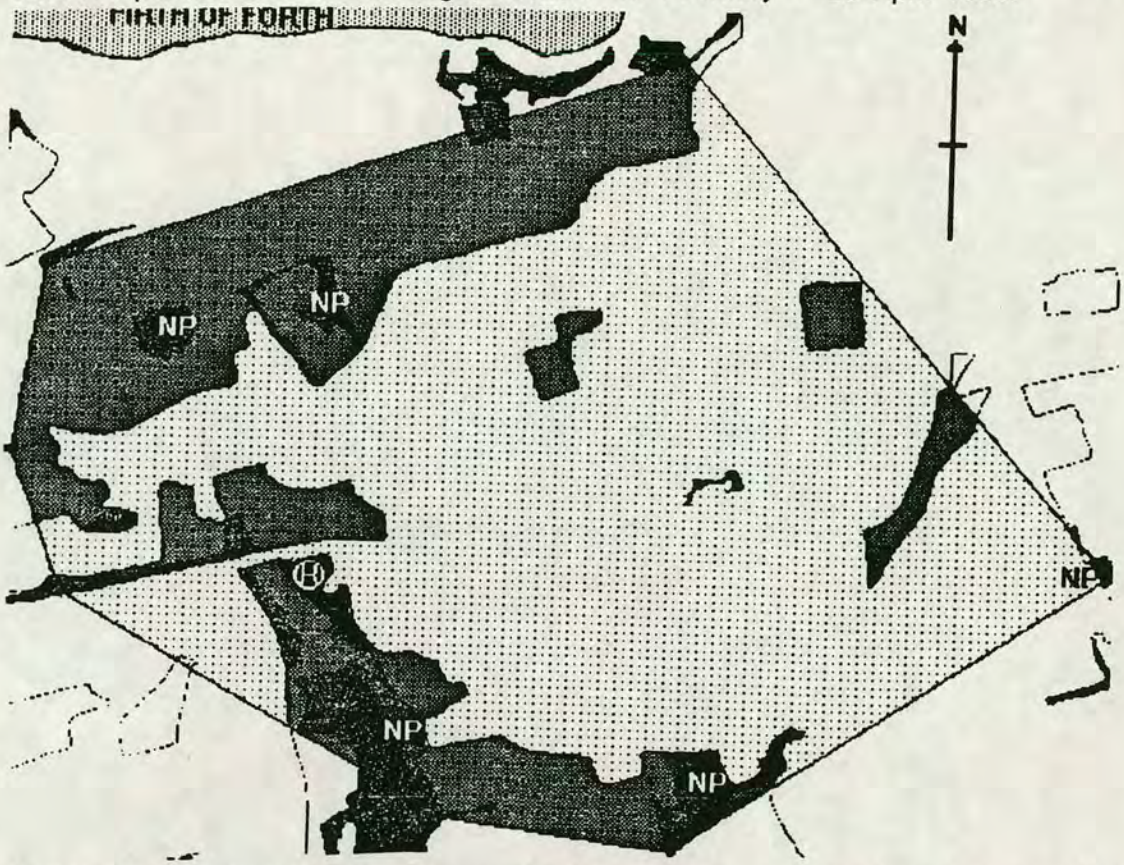
Appendix 2, Figure 4.8 Range (437 hectares) of a breeding, adult male Sparrowhawk in Edinburgh tracked 02 April - 04 May 1988. This individual bred with a yearling female.



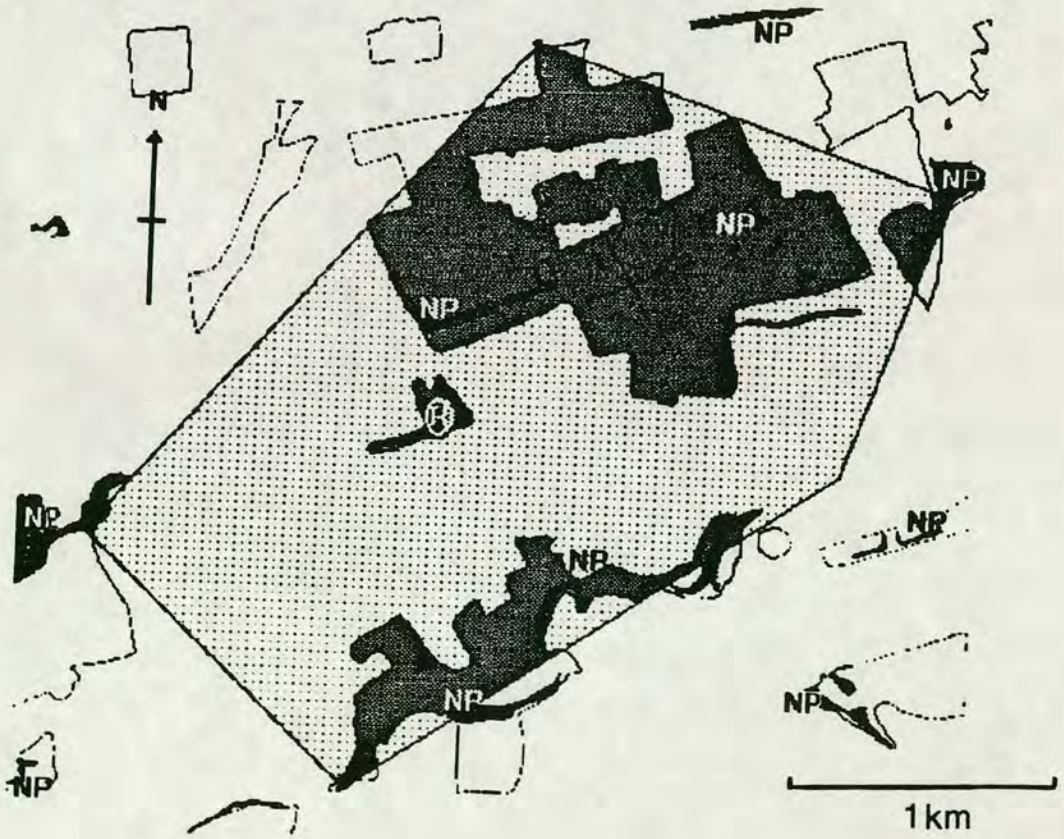
Appendix 2, Figure 4.9 Range (684 hectares) of a breeding, adult female Sparrowhawk in Edinburgh, tracked 18 March - 21 May 1987. This individual was paired with an adult male, but was shot prior to egg-laying. She was replaced by a yearling femle which bred successfully in that year.



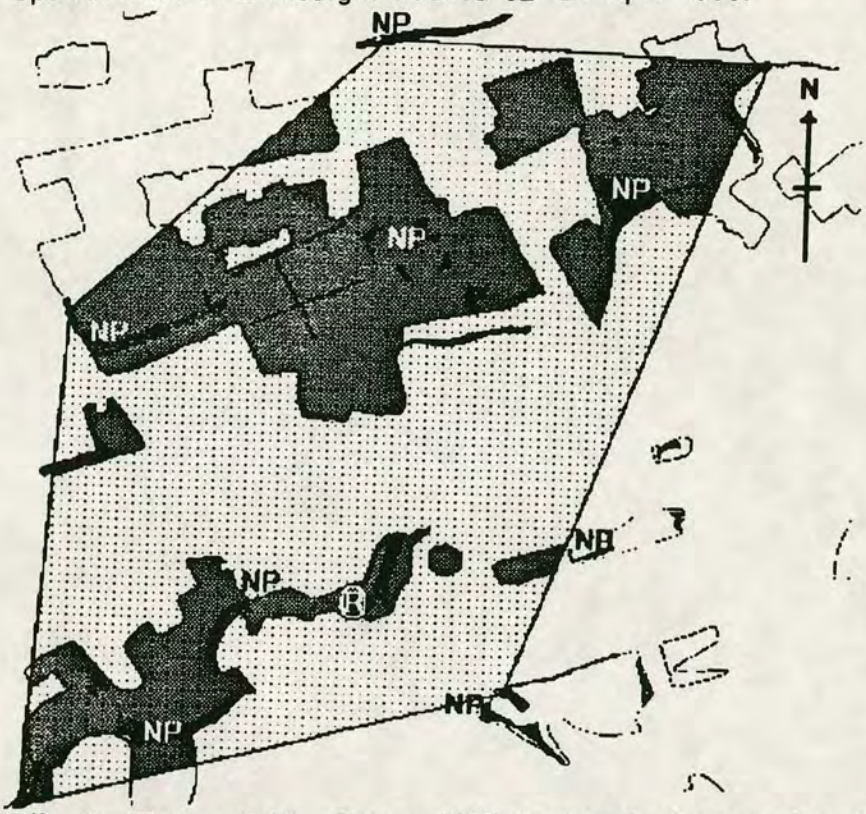
Appendix 2, Figure 4.10 Range (989 hectares) of a non-breeding, yearling female Sparrowhawk in Edinburgh, tracked 12 February - 26 April 1988.



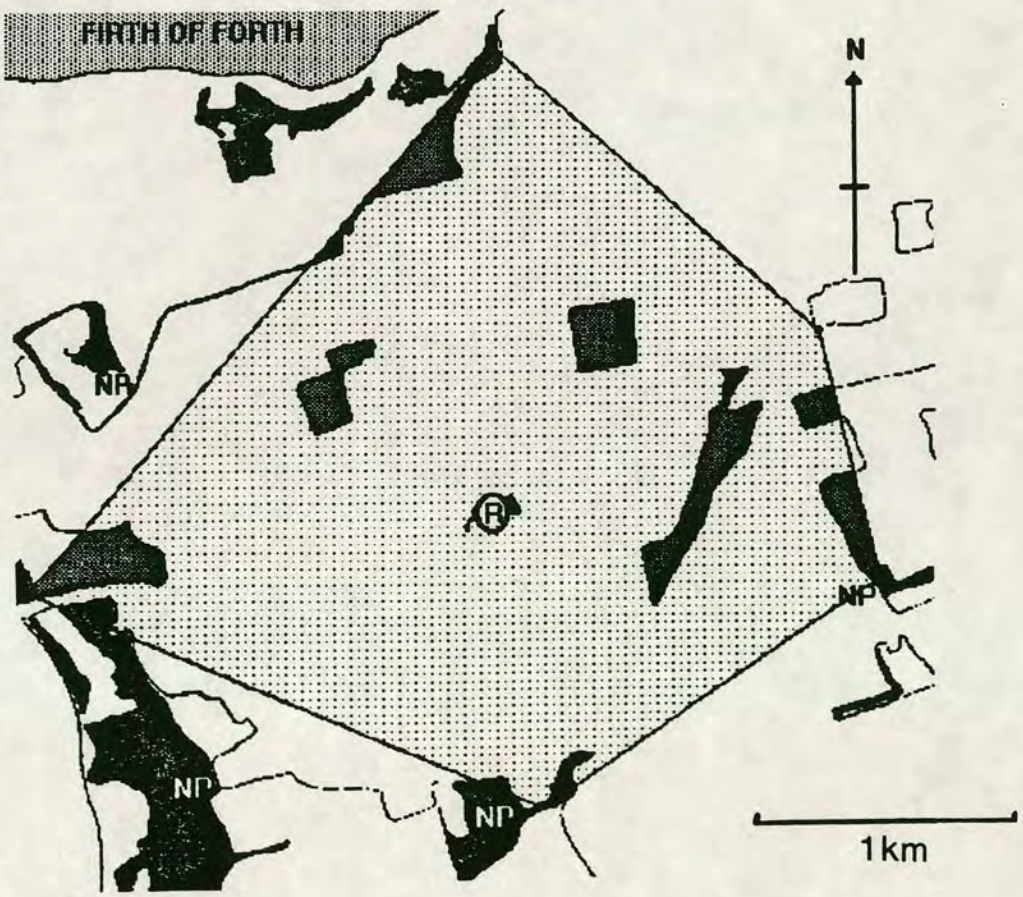
Appendix 2, Figure 4.11 Range (594 hectares) of a non-breeding, yearling male in Edinburgh, tracked 25 February - 18 April 1988.



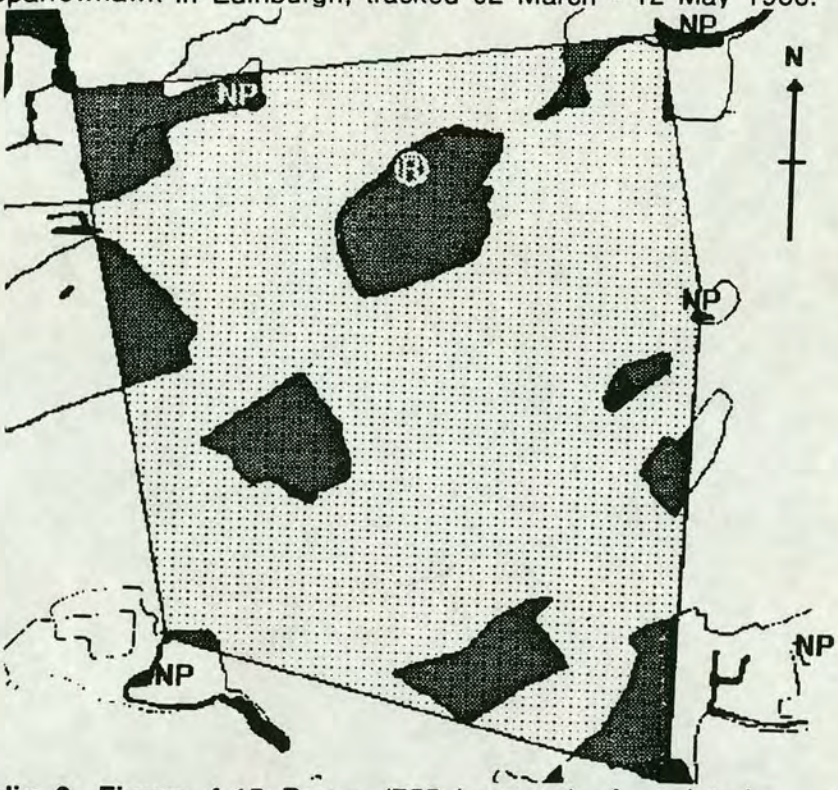
Appendix 2, Figure 4.12 Range (671 hectares) of a non-breeding, yearling male Sparrowhawk in Edinburgh. tracked 02 -28 April 1988.



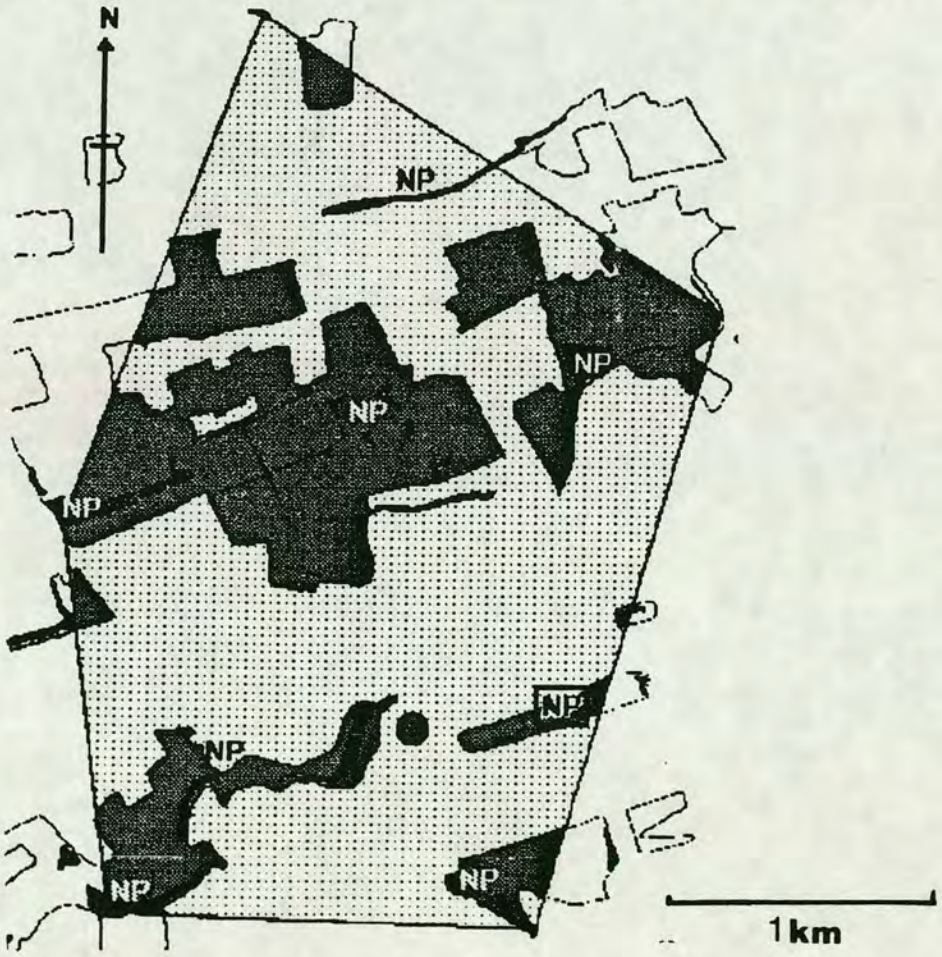
Appendix 2, Figure 4.13 Range (653 hectares) of a non-breeding, yearling male Sparrowhawk in Edinburgh, tracked from 25 February - 15 May 1988.



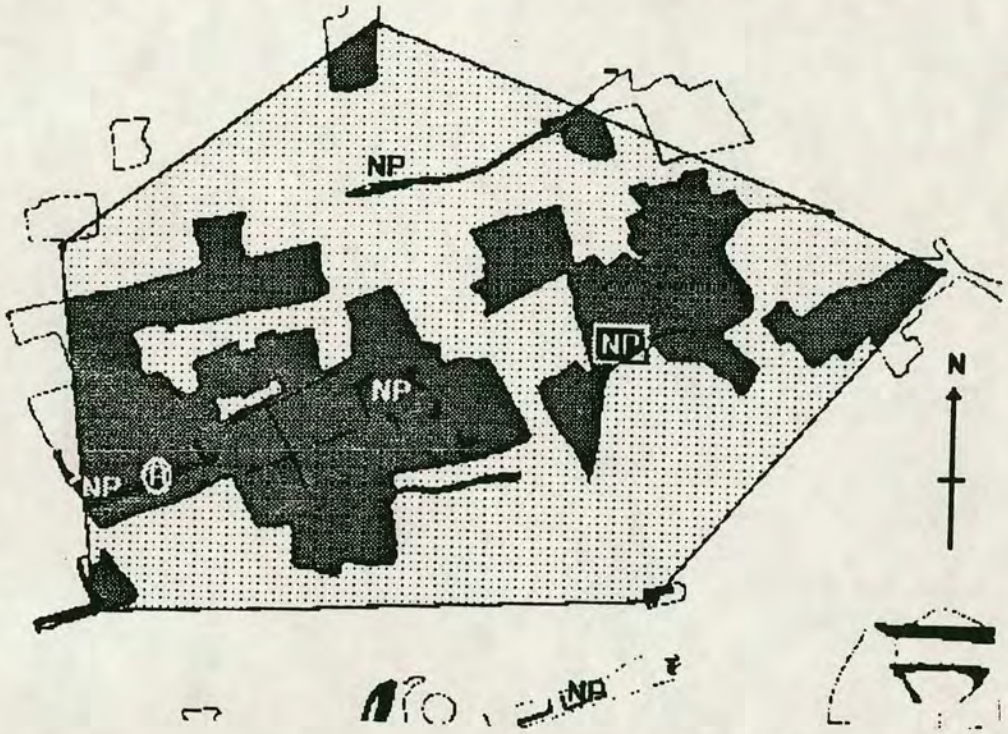
Appendix 2, Figure 4.14 Range (660 hectares) of a non-breeding, yearling male Sparrowhawk in Edinburgh, tracked 02 March - 12 May 1988.



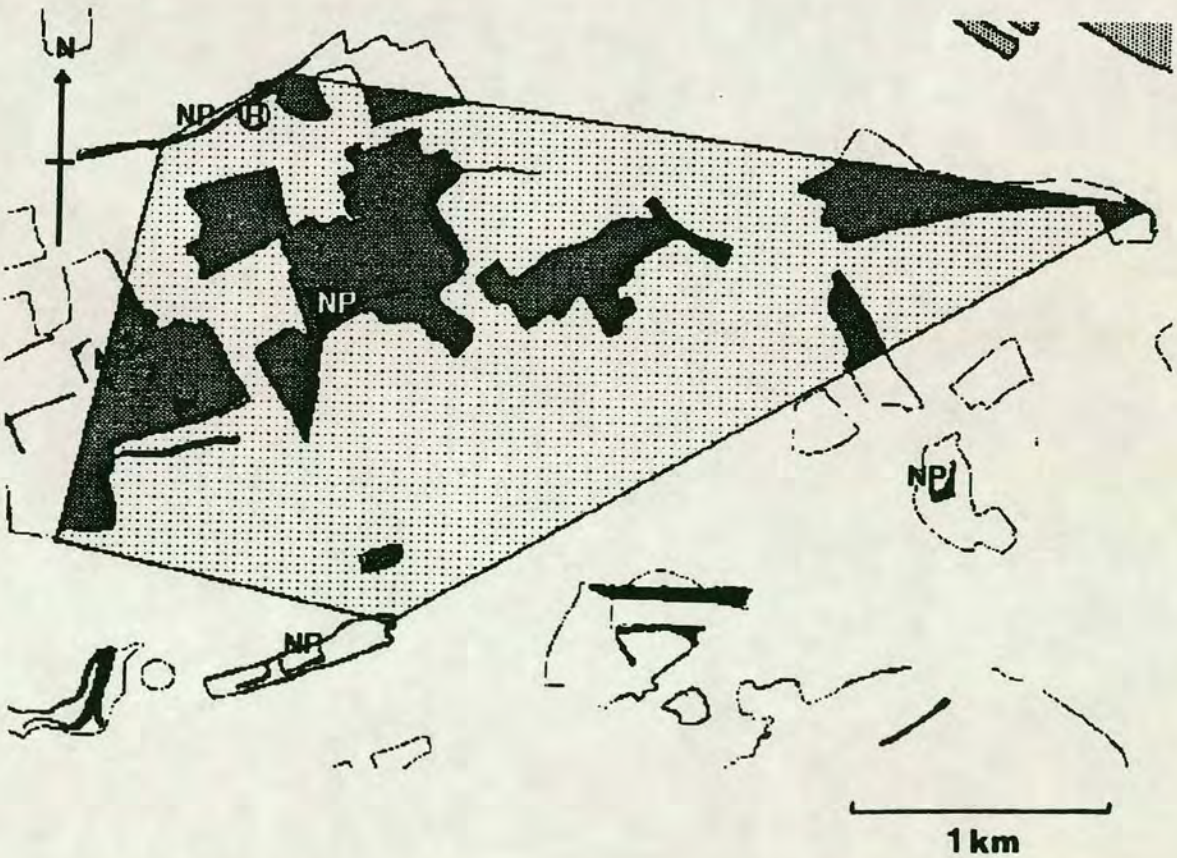
Appendix 2, Figure 4.15 Range (755 hectares) of a wintering, yearling female Sparrowhawk in Edinburgh, tracked 24 November 1987 - 24 January 1988. This individual was ringed as a nestling 51 km from the study area, and bred in 1988 with an adult male.



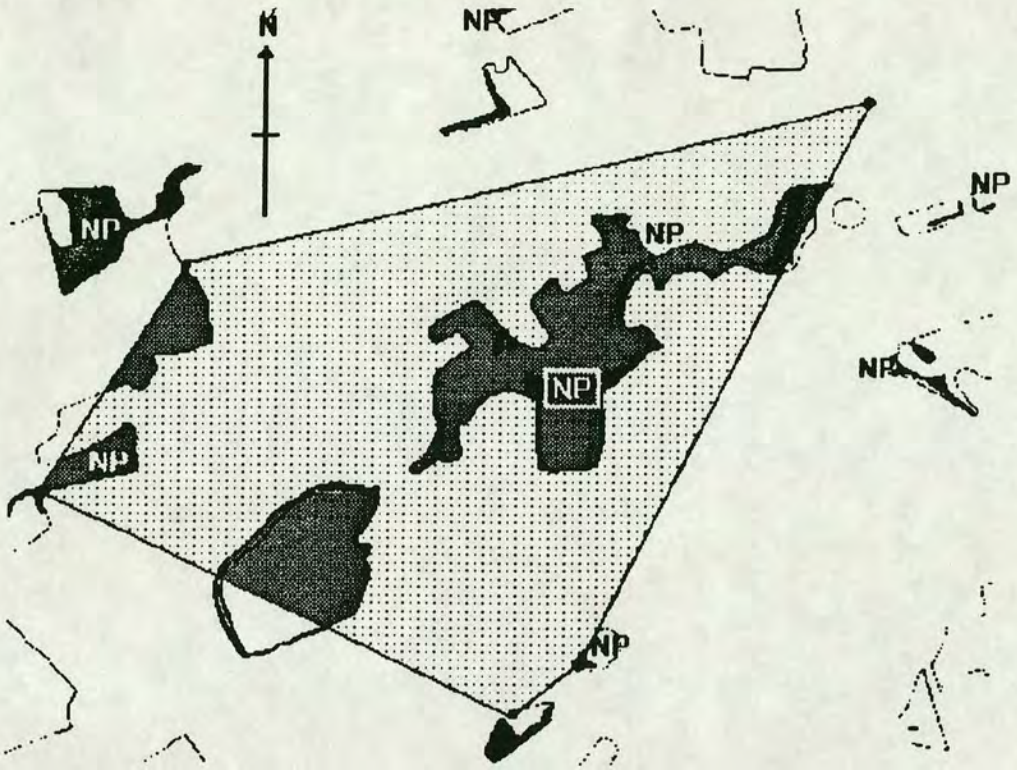
Appendix 2,Figure 4.16 Range (618 hectares) of a wintering, adult female Sparrowhawk in Edinburgh, tracked 16 November 1987 - 1 February 1988. This individual bred succcessfully with an adult male in 1988.



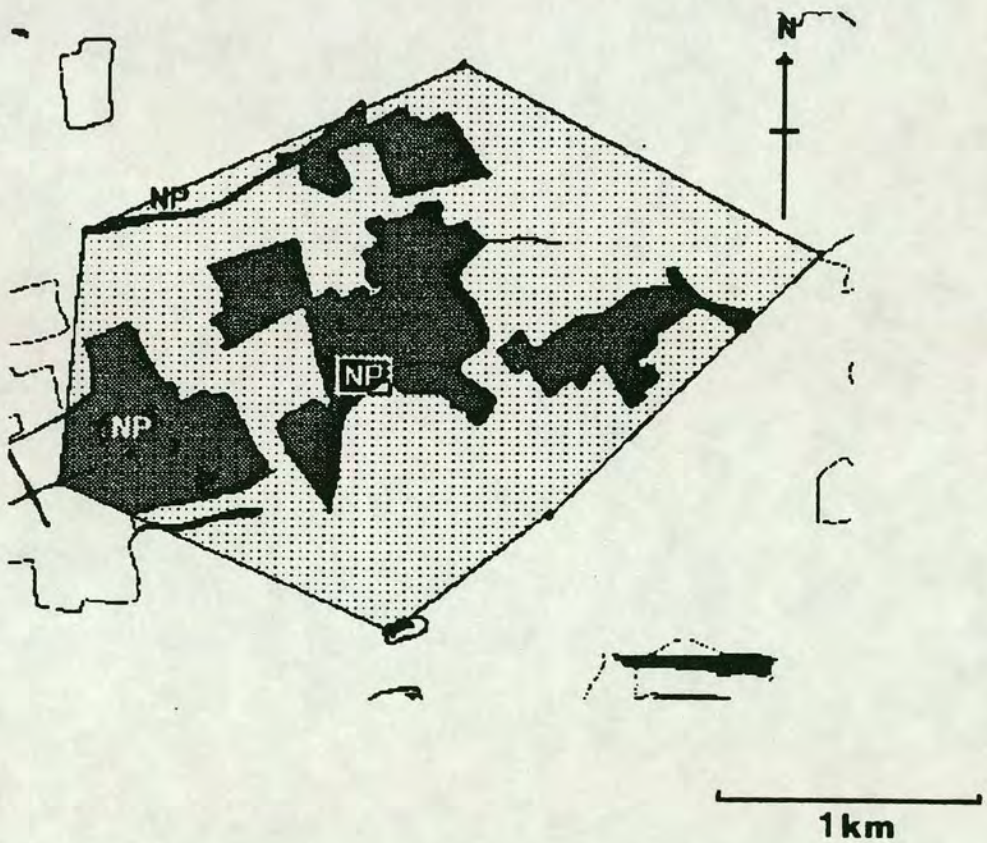
Appendix 2, Figure 4.17 Range (615 hectares) of a wintering, yearling female Sparrowhawk in Edinburgh, tracked 7 November 1987 - 2 January 1988.



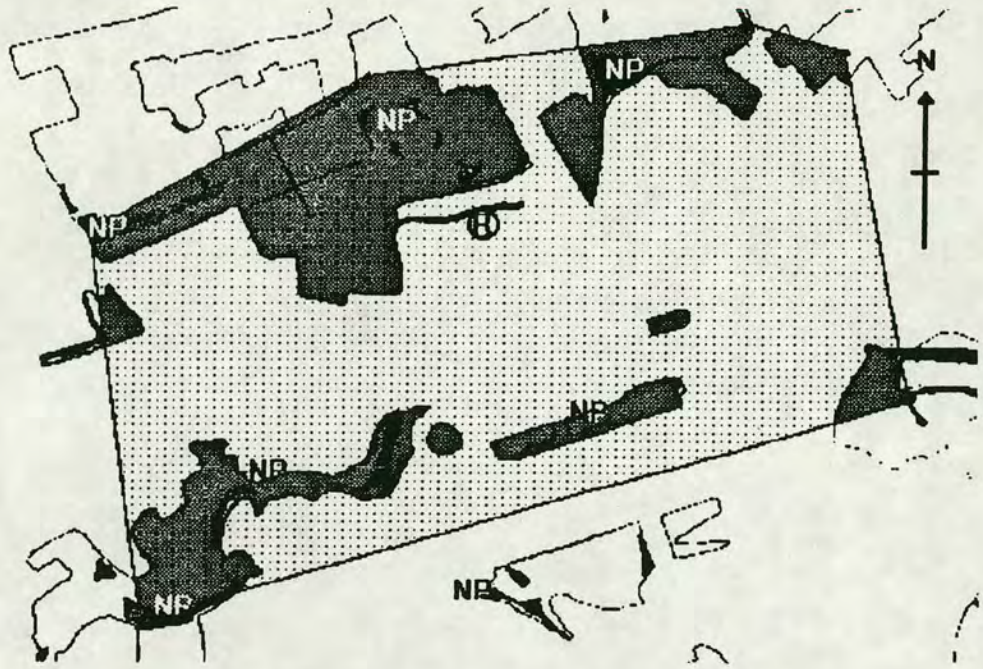
Appendix 2, Figure 4.18 Range (471 hectares) of a wintering, adult male Sparrowhawk in Edinburgh tracked 22 November - 10 December 1987.



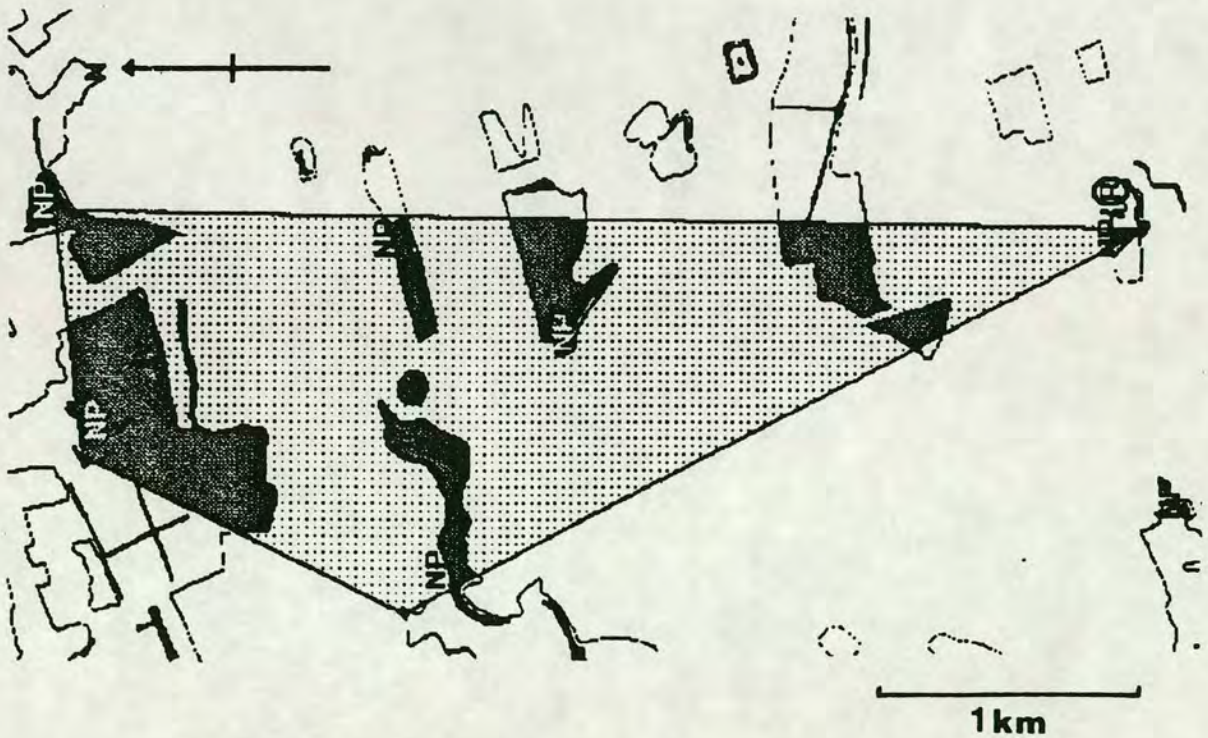
Appendix 2, Figure 4.19 Range (409 hectares) of a wintering, yearling male Sparrowhawk in Edinburgh tracked 06 - 10 December 1987. This individual bred in 1988 with an adult female.



Appendix 2, Figure 4.20 Range (607 hectares) of a wintering, yearling male Sparowhawk in Edinburgh, tracked 22 November -17 January 1988.



Appendix 2, Figure 4.21 Range (454 hectares) of a wintering, yearling male Sparrowhawk in Edinburgh, tracked 27 November - 20 December 1988.



Appendix 2, Figure 4.22 Map of ranges of 6 males which occupied adjacent territories in 1987 and 1988 illustating the extent to which they overlap in the pre-egg laying period. It may be that within either of those years, the ranges were somewhat more exclusive. Many of the males bred in the same place, but were not radio-marked in both years. Nesting places are marked with a Arabic numeral. The boundries of the ranges of the males breeding at those places are marked with the corresponding Roman numeral.